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RESEARCH ARTICLE

Genetic studies and mapping of quantitative trait loci (QTL) for yield and yield-related traits in vegetable and seed soybean (*Glycine max* L.) -derived populations

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Abstract

Understanding the genetic control of seed yield and yield-related traits is essential for its targeted manipulation and genetic improvement. In this study, vegetable soybean (*Glycine max* L.) genotype- AGS457, and seed soybean genotype- SKAF148 derived F_2 and $F_{2:3}$ populations were phenotyped in the field for yield and yield-related traits and were genotyped with SSR markers for understanding genetic control and mapping of the yield and yield related traits. Normal frequency distribution of the traits indicated polygenic inheritance of yield and yield-related traits under study. The genetic map constructed with 105 polymorphic SSR markers covered 2005.7cM across 20 chromosomes of soybean. In the F_2 generation of the crosses, 11 distinct QTLs were mapped for the yield and yield-related traits with any single QTL explaining 4.9 to 27.93% phenotypic variations of the trait concerned. The 11 QTLs were mapped on 9 different chromosomes viz., 5, 6, 7, 9, 11, 13, 16, 18 and 19. Similarly, 19 QTLs were mapped in the $F_{2:3}$ population with phenotypic variation explained (PVE) by any single QTL ranging from 3.27 to 23.14%. The QTLs in the $F_{2:3}$ population were mapped on 12 different chromosomes viz., 1, 3, 4, 6, 7, 10, 11, 12, 13, 16, 18 and 20. Three QTLs, one each for plant height at maturity (qPHM11-1), two-seeded pod length (qTSPL16-1) and seed weight per plant (qSWPP6-1) were consistent across F_2 and $F_{2:3}$ generations. Most of the 19 QTLs mapped in this study were novel ones. The knowledge of genetic control of the target traits and their mapping with SSR markers would facilitate the deployment of these QTLs for enhancing yield and other related traits in soybean.

Keywords: Soybean, yield-related traits, F_2 population, $F_{2:3}$ population, simple sequence repeat, quantitative trait loci.

Introduction

The primary goal of soybean [*Glycine max* (L.) Merrill.] breeding is to increase the yield and quality of the produce. The expression and interrelationship of various plant growth factors such as plant height, days to flowering, days to maturity, number of pods per plant, pod length, pod width, and seed size contribute towards seed yield. The plant growth components are primarily quantitative in nature and heavily influenced by the environment (Ainsworth et al. 2012). Therefore, understanding their genetic basis through conventional approaches is difficult and error-prone. However, molecular markers, which are immune to environmental influences, can effectively identify chromosomal regions regulating the expression of complex quantitative traits. Understanding the genetic control of seed yield and yield-related traits would facilitate effective selection procedures, such as marker-assisted selection (MAS). Therefore, it is critical to investigate the genes/QTLs that govern seed yield and its related traits with molecular markers. Among others, the simple sequence repeats (SSR) markers, which are hypervariable, multi-allelic, co-dominant, highly repeatable, and have huge genome coverage, are widely used in soybean molecular breeding (Danesh et al. 1998). However, markers need validation for their usefulness

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in determining the target phenotype across independent populations with diverse genetic origins (Collard et al. 2005). QTLs that are stable and validated are important for effective MAS (Song et al. 2004).

Vegetable soybean varieties have extra-large and highly sweet seeds (Kumar et al. 2022). Some of the vegetable soybean varieties have a pleasant aroma and attractive grain color that fetches higher prices in the market. Seed weight (seed size) is a significant component of soybean yield and is generally connected with seed yield. Seed size is connected to seed yield (Burton 1987; Kumar et al. 2023), and is crucial in the manufacturing of soy-based products (Hoeck et al. 2003); small-seeded soybeans are preferred for producing high-quality soybean sprouts and natto, while large-seeded soybeans are preferred for producing tofu, edamame, and miso (Wilson 1995).

To date, a number of QTLs for seed yield-related traits such as the number of pods per plant (Sun et al. 2006; Zhang et al. 2010; Daraghi et al. 2014), and seed weight (Hoeck et al. 2003; Hyten et al. 2004; Panthee et al. 2005; Dargahi et al. 2014; Zhang et al. 2021), seed viability (Saini et al. 2023) have been mapped. Similarly, marker-assisted backcross breeding approach has also been used to improve the quality of soybean (Pawale et al. 2021). However, mapping of QTL for yield and yield-related traits involving vegetable and seed soybean is meagre. Therefore, an attempt was made to map and analyze the QTL for yield and yield related traits in an F_2 and $F_{2:3}$ population derived from vegetable soybean variety AGS457 and seed soybean genotype SKAF148.

Materials and methods

Plant materials

The study was conducted with two soybean genotypes, AGS 457 and SKAF 148 and the F_2 and $F_{2:3}$ populations derived from their crosses. The AGS 457 is a large-seeded vegetable soybean genotype, whereas SKAF 148 is a small-seeded grain-type soybean. Both the genotypes varied significantly for seed weight and the number of pods per plant. The F_2 generation consisting of 237 plants along with the parental genotypes were grown during *kharif* season of 2020, i.e., July – November 2020 in the experimental field of the Indian Agricultural Research Institute (IARI), New Delhi, India. Data were collected from each plant individually. Young leaves were collected from each F_2 plant and were used to extract DNA for molecular genotyping of the plants. Each of the 237 F_2 plants was harvested individually and the $F_{2:3}$ seeds were sown in family row during July-November 2021 in the IARI, New Delhi experimental field. The $F_{2:3}$ plants were evaluated phenotypically by collecting data from 5 randomly selected from each family row separately.

Trait measurement

The traits measured from the F_2 and the $F_{2:3}$ plants include- Plant height (PH), No. of pods per plant (NPPP), Two-seed pod length (TSPL), Two-seed pod width (TSPW), No. of seeds per plant (NSPP), and Seed weight per plant (SWPP). Software package 'R' (R Core Team 2013) was used to compute Pearson phenotypic correlation coefficients among traits under study.

DNA extraction and SSR genotyping

Using a modified CTAB approach described by Lodhi et al. (1994), genomic DNA was isolated from the young leaves of the two parents and each F_2 plant. The quality of DNA was checked on a 0.8% agarose gel stained with ethidium bromide. A set of 580 SSR markers distributed nearly uniformly throughout the 20 genetic linkage groups of the consensus soybean genetic linkage map published by Cregan et al. (1999) and Song et al. (2004) were used to study polymorphism between the parental genotypes. The SSR markers polymorphic between the parents AGS 457 and SKAF 148 were employed to genotype the F_2 plants.

Map construction and QTL detection

To create the linkage map and detect QTLs, we utilized the software QTL IciMapping V4.2. The linkage map connecting the markers was built using a minimum LOD score of 2.5 and a maximum genetic distance of 50 cM. Kosambi's mapping function (Kosambi 1944) was used to calculate map distances. The QTL analysis was carried out using the composite interval mapping approach (CIM) (Zeng, 1994). A LOD score of 2.5 was kept to certify the presence of a QTL in a certain genomic area. When the LOD score of the QTL exceeded the threshold value, it was considered a significant one.

Results

Phenotypic variation in parents and the segregating population

All traits tested showed a significant difference between the two parents, AGS 457 and SKAF 148 (Table 1). The frequency distribution of the F_2 generation data of all the traits showed that all traits except seed weight per plant were distributed normally (Fig. 1). It indicated polygenic control of these traits. Further, transgressive segregants were observed in all the traits. Significant correlation coefficients across yield-related traits varied from -0.26 to 0.95 in the F_2 population and from -0.21 to 0.68 in the $F_{2:3}$ population. (Table 2). Phenotypic traits such as the number of pods per plant, two seeds pod length, number of seeds per plant, and the Seed weight per plant were found to be positively correlated, indicating their contribution towards yield per plant.

Table 1. Descriptive statistics of the evaluated quantitative traits in the parents, F_2 population and $F_{2:3}$ populations

Traits	Parental genotype		Parental Difference	F_2 Population		$F_{2:3}$ Population	
	AGS 457	SKAF 148		Range	Mean± SD	Range	Mean± SD
PH	52.5	35.0	17.5	34.4–54.4	45.17 ± 5.32	35.3–57.1	45.9 ± 4.92
NPPP	40.0	21.0	19.0	5.0–47.0	22.65 ± 10.52	10.0–42.0	27.5 ± 6.68
TSPL	4.2	3.2	1.0	2.35–4.45	3.56 ± 0.41	2.7–4.5	3.6 ± 0.4
TSPW	1.2	0.8	0.4	0.6–1.25	0.87 ± 0.14	0.7–1.3	1.0 ± 0.14
NSPP	62.0	36.0	26.0	8.0–101.0	45.87 ± 23.82	27.0–70.0	52.0 ± 10.0
SWPP	17.23	3.79	13.44	0.83–17.17	6.41 ± 4.07	3.8–15.8	8.1 ± 2.57

PH = Plant height (cm), NPPP = Number of pods per plant, TSPL = Two seed pod length (cm), TSPW = Two seed pod width (cm), NSPP = Number of seeds per plant and SWPP = Seed weight per plant (g)

Table 2. Pearson correlation coefficients among yield-related traits in F_2 and $F_{2:3}$ populations

Traits	PH	NPPP	TSPL	TSPW	NSPP	SWPP
F_2 Population						
PH	1	0.216NS	-0.260*	-0.042NS	0.172NS	0.127NS
NPPP	0.216NS	1	0.143NS	-0.015NS	0.946**	0.838**
TSPL	-0.260*	0.143NS	1	0.150NS	0.196NS	0.279*
TSPW	-0.042NS	-0.015NS	0.150NS	1	-0.097NS	-0.090NS
NSPP	0.172NS	0.946**	0.196NS	-0.097NS	1	0.906**
SWPP	0.127NS	0.838**	0.279*	-0.090NS	0.906**	1
$F_{2:3}$ Population						
PH	1	0.227**	-0.206**	0.164*	0.180**	0.125NS
NPPP	0.227**	1	0.099NS	-0.023NS	0.676**	0.394**
TSPL	-0.206**	0.099NS	1	0.057NS	0.115NS	0.211**
TSPW	0.164*	-0.023NS	0.057NS	1	-0.003NS	0.022NS
NSPP	0.180**	0.676**	0.115NS	-0.003NS	1	0.637**
SWPP	0.125NS	0.394**	0.211**	0.022NS	0.637**	1

*,**, Significant at 0.05, 0.01 levels, respectively, NS = Non-Significant.

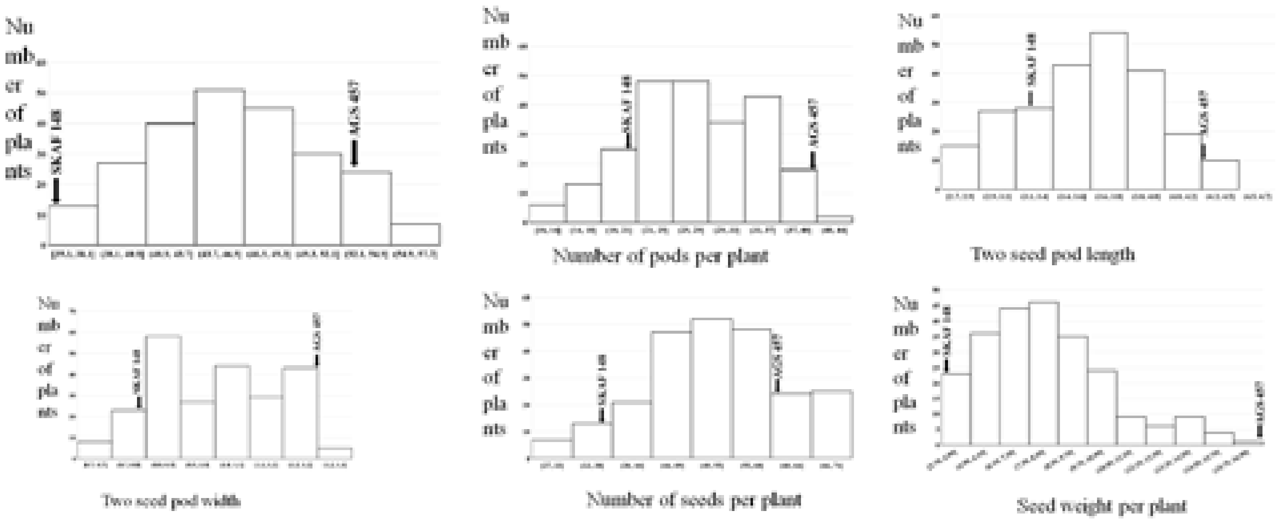

Fig. 1. Frequency distributions of yield-related traits in the $F_{2:3}$ population derived from the AGS 457 X SKAF 148 cross. Parental means are indicated with arrows

Linkage map construction

A set of 580 SSR markers were used to screen the two parents for genetic polymorphism. One hundred and five out of 580 SSR markers were polymorphic, indicating the polymorphism between the parental genotypes to be 18.1%. Rejecting the 11 markers that showed ambiguous and distorted bands, rest 94 polymorphic markers were used for genotyping the F_2 generation plants. The selected markers found to follow the placement and order as given in the reference genetic maps (http://soybase.agron.iastate.edu/). Based on the F_2 generation data, the linkage map was constructed and all 94 markers were assigned to 20 different linkage groups. Although the order of the markers remained the same, yet the map distance between the markers in the newly constructed map was found to vary from the original map insignificantly. The coverage of the new linkage map (2005.7 cM) to the original soybean genome map (2523.6 cM) was 79.5%, which is quite high.

QTL analysis

QTL analysis was carried out using data from the F_2 and $F_{2:3}$ populations. All the QTLs identified in the F_2 and $F_{2:3}$ mapping populations were depicted in Tables 3 and 4, respectively. Using Inclusive Composite Interval Mapping (ICIM) approach, 11 distinct QTLs were identified for all traits in the F_2 population (Fig 2). The phenotypic variation explained (PVE) by any single QTLs ranged from 4.9 to 27.93%. The QTLs were distributed across nine of the 20 different chromosomes viz., chr.5, 6, 7, 9, 11, 13, 16, 18, and 19. Chromosome 9 was found to harbour three QTLs while other QTLs were found on one chromosome each.

In the $F_{2:3}$ populations, a total of 19 QTLs were found across all traits under testing. The PVE of any one QTL is between 3.27 and 23.14%. The 19 QTLs were found to distribute on 12 different chromosomes viz., 1, 3, 4, 6, 7, 10, 11, 12, 13, 16, 18 and 20. The highest number of QTLs i.e., 3 QTLs was mapped on chromosome 20. Two QTL each were mapped on chromosomes 4, 11, 12, 13, and 16. The rest 6 QTLs were mapped on 6 different chromosomes.

Five QTLs for plant height at maturity were found on chromosomes 5, 7, 11, 13, and 19 in the F_2 population, while four QTLs were found on chromosomes 1, 4, 11, and 18 in the $F_{2:3}$ populations. In both populations, the allele from the short genotype SKAF 148 found to contribute towards lowering the plant height. Two major QTL for plant height at maturity i.e. qPh4-1 and qPh11-1 were mapped on chromosomes 4 and 11, respectively. The QTL qPh4-1 on chromosome 4 was mapped in the marker interval Sct_186-Sat_207 with a LOD score of 4.29 with PVE 19.68%. Another major QTL, qPH11-1, was mapped on chromosome 11 in the Satt484-Sat_270 interval, with a LOD score of 3.21 and accounting for 17.07% of the phenotypic variation. This QTL qPH11-1 was found in the F_2 and $F_{2:3}$ populations and hence was considered a consistent QTL (Table 5). One QTL was mapped

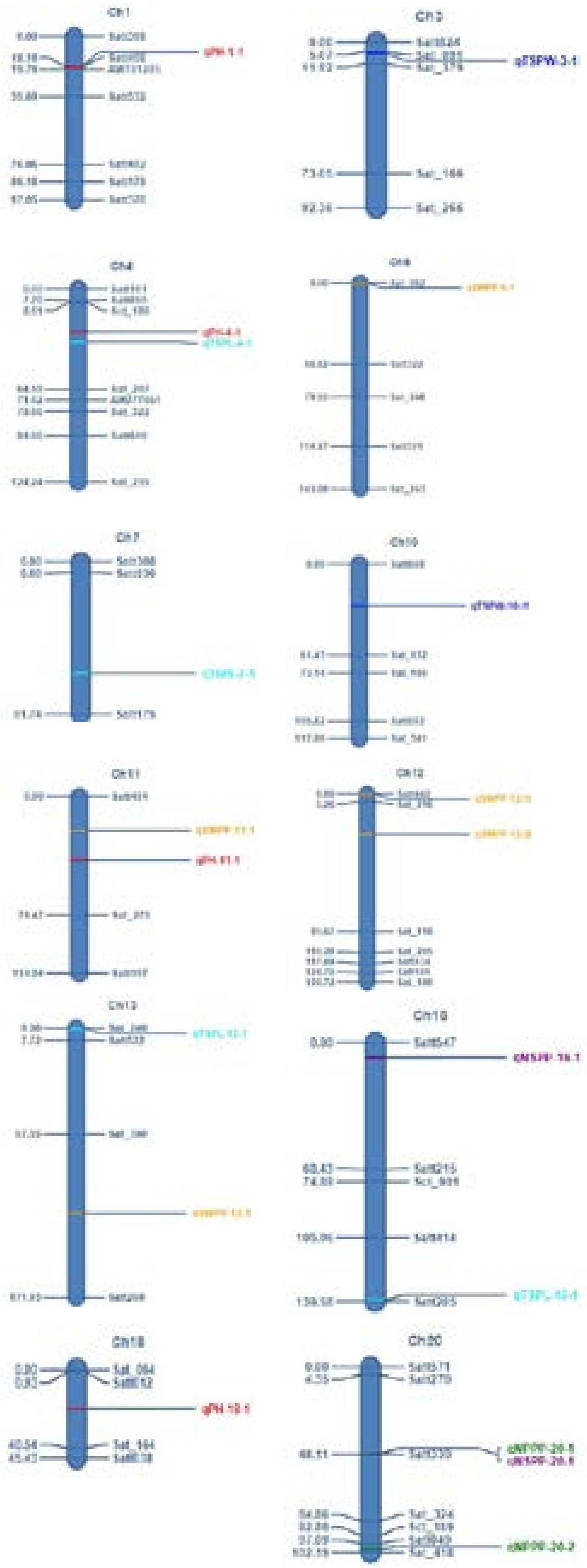

Fig. 2. **QTL locations associated with yield-related traits in the $F_{2:3}$** populations resulting from the AGS 457 X SKAF 148

Table 3. QTLs identified for yield-related traits in the F_2 mapping population derived from AGS 457 X SKAF 148

Trait	QTL	Chromosome/ LG	Position (cM)	Marker Interval	LOD	Additive	Dominance	R^2 (%)
Plant height	qPH-5-1	5 (A1)	111	Satt050-Satt684	5.67	5.24	4.52	6.09
	qPH-7-1	7 (M)	39	Satt636-Satt175	2.96	-3.02	6.68	4.99
	qPH-11-1	11 (B1)	41	Satt484-Sat_270	3.05	-1.03	-8.52	4.90
	qPH-13-1	13 (F)	39	Satt269-Sat_240	2.62	2.27	7.88	5.02
	qPH-19-1	19 (L)	25	Sat_340-Sat_286	3.05	-5.95	1.56	5.47
No. of pods per plant	qNPPP-9-1	9 (K)	38	Satt196-Satt337	3.38	-9.69	-6.79	14.93
Two seed pod length	qTSPL-16-1	16 (J)	139	Satt414-Satt285	4.88	0.35	0.06	27.93
Two seed pod width	qTSPW-18-1	18 (G)	6	Satt012-Sat_164	3.00	-0.08	-0.07	16.20
No. of seeds per plant	qNSPP-9-1	9 (K)	37	Satt196-Satt337	5.57	-23.44	-20.79	14.00
Seed weight per plant	qSWPP-6-1	6 (C2)	0	Sat_062-Satt322	2.76	4.42	-1.81	19.07
	qSWPP-9-1	9 (K)	60	Satt337-Satt260	2.68	-2.09	-0.39	5.27

Table 4. QTLs identified for yield-related traits in the $F_{2:3}$ mapping population derived from AGS 457 X SKAF 148

Trait	QTL	Chromosome/ LG	Position (cM)	Marker Interval	LOD	Additive	Dominance	R^2(%)
Plant height	qPH-1-1	1 (D1a)	18	Satt368-Satt408	2.76	-0.18	3.84	4.77
	qPH-4-1	4 (C1)	28	Sct_186-Sat_207	4.29	5.80	0.47	19.68
	qPH-11-1	11 (B1)	41	Satt484-Sat_270	3.21	-5.27	0.84	17.07
	qPH-18-1	18 (G)	20	Satt012-Sat_164	2.69	3.54	3.42	10.09
No. of pods per plant	qNPPP-20-1	20 (I)	48	Satt270-Satt330	4.15	4.20	0.42	23.14
	qNPPP-20-2	20 (I)	100	Satt049-Sat_418	3.15	3.83	-1.57	17.12
Two seed pod length	qTSPL-4-1	4 (C1)	34	Sct_186-Sat_207	3.20	-0.10	0.45	15.43
	qTSPL-7-1	7 (M)	67	Satt636-Satt175	3.52	0.13	0.45	15.96
	qTSPL-13-1	13 (F)	0	Sat_240-Satt522	6.34	0.28	-0.07	12.71
	qTSPL-16-1	16 (J)	139	Satt414-Satt285	4.50	0.21	-0.16	8.03
Two seed pod width	qTSPW-3-1	3 (N)	6	Sat_091-Sat_379	3.16	0.00	0.12	4.02
	qTSPW-10-1	10 (O)	28	Satt608-Sat_132	2.54	-0.01	0.21	12.86
No. of seeds per plant	qNSPP-16-1	16 (J)	8	Satt547-Satt215	2.65	6.64	-1.86	19.37
	qNSPP-20-1	20 (I)	48	Satt270-Satt330	3.76	6.02	-2.53	18.61
Seed weight per plant	qSWPP-6-1	6 (C2)	0	Sat_062-Satt322	3.13	0.80	2.21	8.44
	qSWPP-11-1	11 (B1)	22	Satt484-Sat_270	3.51	-1.73	-3.84	11.26
	qSWPP-12-1	12 (H)	0	Satt442-Sat_216	2.96	-1.09	-1.96	3.27
	qSWPP-12-2	12 (H)	28	Sat_216-Sat_118	3.14	-1.89	-3.35	10.43
	qSWPP-13-1	13 (F)	118	Sat_390-Satt269	3.05	2.11	-3.53	10.53

on chromosome 9 in the Satt196-Satt337 interval of the F_2 plants for the number of pods per plant. Similarly, in the $F_{2:3}$ population, two large QTLs were mapped on chromosome 20 for the same trait. The alleles from the genotype SKAF 148 were found to reduce the number of pods per plant. The marker interval, Satt270-Satt330, contained one major QTL, qNPP20-1, with a LOD score of 4.15 and explaining 23.14% of the phenotypic variation. Another major QTL for the same trait, i.e., qNPP20-2, was mapped in the Satt049-Sat_418 interval that had an LOD score of 3.15 and explained 17.12% of the phenotypic variations.

One QTL for two-seed pod length was observed on chromosome 16 in the Satt414-Satt285 interval in an F_2 population, while four QTLs for two-seed pod length were mapped on chromosomes 4, 7, 13, and 16, where AGS 457 alleles contributed towards increasing the pod length. The QTL for two-seed pod length on chromosomes 4 and 7 were major QTLs with LOD scores of 3.2 and 3.52 and explained 15.43 and 15.96% of the phenotypic variations, respectively. One QTL, qTSPL16-1, was found on chromosome 16 in the Satt414-Satt285 interval, explaining 8.03% of phenotypic variation and can be regarded as a stable QTL (Table 5). One QTL for two seed pod width was observed on chromosome 18 in the Satt012-Sat _164 interval in the F_2 population, while two QTLs were found in the $F_{2:3}$ population on chromosomes 3 and 10 where SKAF 148 alleles lowered the trait. One large QTL was found on chromosome 10 in the Satt608-Sat_132 interval, with a LOD score of 2.54 and accounting for 12.86% of the phenotypic variance. In the F_2 population, one QTL for the number of seeds per plant was found on chromosome 9 in the Satt196-Satt337 interval, while two large QTLs were found on chromosomes 16 and 20 in the $F_{2:3}$ population. AGS 457 alleles elevated the phenotype at these QTLs. One large QTL was discovered on chromosome 16 in the Satt547-Satt215 interval, with a LOD score of 2.65 explaining 19.37% of the phenotypic variation. Another significant QTL for seed number per plant was discovered on chromosome 20 in the Satt270-Satt330 interval, with a LOD score of 3.76 explaining 18.61 % of the phenotypic variation.

For seed weight per plant, two QTLs were mapped on chromosomes 6 and 9 in the F_2 population plants. Conversely, in the $F_{2:3}$ populations, five QTLs were mapped for the same on chromosomes 6, 11, 12, and 13. The alleles from AGS 457 were found to contribute positively to increasing the seed weight per plant at these QTLs. The QTL for seed weight per plant (qSWP) mapped on chromosomes 11, 12, and 13 were all major QTLs with PVE 11.26%, 10.53%, and 10.43%, respectively (Table 4). One QTL for the same seed trait mapped on chromosome 6, i.e., qSWP6-1 with PVE 8.44% appeared as a stable QTL (Table 5).

Discussion

Although it belongs to the same species max, yet the vegetable and seed soybean represents two different classes of soybean that vary for a host of traits, including seed size, pod size, taste, yield, etc. Moreover, both types are harvested at varying period of maturity- vegetable soybeans are harvested once the pods are fully developed, while seed soybeans are harvested when the pods are turned yellow and dried. The phenotypic diversity of both the types in one hand and their cross compatibility on the other makes it an appropriate material for studying genetic control and mapping of various traits in soybean. This study used the vegetable soybean genotype AGS457 and seed soybean genotype SKAF148 to develop mapping population, understanding genetics of yield and yield-related traits and their mapping using SSR markers.

In usual mapping studies, F_2 population is commonly used; however, owing to its single cycle of meiosis in the development of F_2, it is not considered an ideal population for mapping complex traits. Therefore, $F_{2:3}$ or RIL population is developed and used preferably and suitably for such studies. In this study, both F_2 and $F_{2:3}$ generation mapping populations were developed by crossing the vegetable and seed soybean genotypes and were used for genetic studies and mapping of morphological traits, including seed yield.

The contrast of traits in the parental genotypes led to the development of wider trait variation in the subsequent generations. A wide range of variability for all the traits was observed in the F_2 and $F_{2:3}$ generations. Further, the variability went beyond the parental range and developed transgressive segregants in the F_2 population, indicating tremendous recombination between the alleles of both parents' genes. Li et al. (2008) and Zhang et al. (2010) also reported transgressive segregants in segregating populations. Recombination of the diverse alleles results in the recombinants, which may exceed parental line of variability. It may deliver desirable recombinants too.

Table 5. Consistent QTLs for yield-related traits discovered in both F_2 and $F_{2:3}$ mapping populations derived from AGS 457 X SKAF 148

Trait	QTL	Chromosome/LG	Position (cM)	Marker Interval	LOD	PVE(%)
Plant height	qPH-11-1	11 (B1)	41	Satt484-Sat_270	3.21	17.07
Two seed pod length	qTSPL-16-1	16 (J)	139	Satt414-Satt285	4.50	8.03
Seed weight per plant	qSWPP-6-1	6 (C2)	0	Sat_062-Satt322	3.13	8.44

Correlation of the traits of interest offers an opportunity for selecting one trait through another. This study observed significant correlation between yield and yield related traits. The correlation coefficients of the traits in the F_2 generation varied from -0.26 to 0.95 while the same in the $F_{2:3}$ population ranged from -0.21 to 0.68. A significant negative correlation was observed between plant height and the two-seed pod length in F_2 and $F_{2:3}$-generation plants, indicating the plant height's negative impact on the pod length. The number of pods per plant, two-seed pod length, number of seeds per plant, and seed weight per plant were found to be positively associated with yield, which indicated their positive and significant role in determining the yield of a plant in soybean (Assefa et al. 2019).

In this study, 9 QTLs were mapped for plant height; 5 QTLs were mapped in the F_2 generation plants, while 4 QTLs were mapped in the $F_{2:3}$ generation plants. One QTL for plant height, i.e., qPH11-1 appeared to a stable one and had high PVE, i.e., 17.07%. Junyi et al. (2007) also mapped a QTL for plant height on chromosome 11. Another QTL for plant height, i.e., qPH1-1 on chromosome 1 found to correspond with the similar QTL reported earlier by Rodrigues et al. (2016). The QTLs reported so far by various workers, including Junyi et al. (2007), Li et al. (2008), Liu et al. (2011), Rodrigues et al. (2016), and Yashpal et al. (2019) were localized on chromosomes 3, 6, and 10. However, this study reported mapping seven new QTLs for plant height on chromosomes 4, 5, 7, 11, 13, 18, and 19. It might have resulted from the extra variation between the parental genotypes used in this study. The height of the parental genotypes used viz., AGS457 and SKAF were 52.5 cm and 35.0 cm, respectively. The great variation in the plant height between the parental genotypes justifies the observation of several QTLs for plant height, including a few novel ones.

Three QTLs were identified for the number of pods per plant; one in the F_2-generation plants and the other two in the $F_{2:3}$-generation plants. The QTL qNPPP20-1 identified in the marker interval of Satt270-Satt330 appeared to be a major QTL, which explained 23.14% of the phenotypic variation for the trait. Further, it corresponded to the QTL reported by Yu et al. (2018). Matching of a QTL with a previously reported one confirms validity of the approach followed and the acceptability of the results obtained in the experiment. Since the PVE of this QTL is very high (23.14%), the QTL deployment is expected to contribute towards increasing the pod number in a plant.

Two-seed pod length and width are two important traits of vegetable soybean that influence overall yield of a plant. No mapping study has yet been conducted for these two traits. In this study, for the first time QTLs were mapped for the two-seed pod length and two-seed pod width. A set of 5 QTLs were mapped on chromosomes 4, 7, 13, and 16 for two-seed pod length. The percentage of phenotypic variance explained by these QTLs ranged from 8.03 to 15.96%. On chromosome 16, one QTL i.e., qTSPL16-1 was mapped, which was detected in both the population i.e., F_2 and $F_{2:3}$. Such QTL may be useful for enhancing the pod length in soybean. Similarly, 3 QTLs were mapped on chromosomes 3, 10, and 18 for two-seed pod width. The QTL qTSPW3-1, which was detected on chromosome 3 in the Sat_091-Sat_379 interval and explained 4.02% of phenotypic variation, corresponded to the QTL discovered by Rathod et al. (2019) for the number of pods per plant. It demonstrates the role of this locus in determining pod width and the number of pods per plant in soybean.

Three QTLs for number of seeds per plant were identified on chromosomes 9, 16, and 20. The percentage of phenotypic variance explained by these QTLs ranged from 14.0 to 19.37%, indicating these to be major QTLs. The QTL qNSPP20-1 in the marker interval Satt270-Satt330 with a LOD score of 3.76 and PVE18.61% corresponded to the QTL already reported by Yang et al. (2013) for the number of four-seed pods. Thus, this QTL influenced the number of seeds per pod and, hence can be considered as a QTL essential for improving yield in soybean.

Soybean seed weight per plant (SWPP) is an essential yield component that affects total seed production in a plant. The current study identified 7 QTLs for seed weight per plant on chromosomes 6, 9, 11, 12, and 13. The QTL qSWPP13-1, found on chromosome 13 in the marker range Sat_390-Satt269, explained 10.53% of phenotypic variance and corresponded to the already reported QTL viz., qSw13-1 (Mian et al. 1996; Yang et al. (2013). Appearance of this QTL across several genetic backgrounds establishes its true nature and suitability for deploying in breeding for yield enhancement in soybean. Similarly, the QTL, qSWPP6-1 on chromosome 6 in the Sat_062-Satt322 interval with PVE 8.44% appeared in both F_2 and $F_{2:3}$ generations and thus exhibited suitability for a breeding program. Liu et al. (2011) discovered two substantial seed weight per plant (SWPP) QTLs on Chromosomes 8 (Satt390) and 10 (Sat_108) that are likely connected to QTLs for seed numbers per pod (SNPP) and pod numbers per plant (PNPP). Chen et al. (2007) identified QTLs for seed weight per plant in a single environment and timepoint on chromosomes 5, 7, and 8. By comparing the QTLs mapped in this study with the previously reported ones, it was found that four novel QTLs for seed weight per plant were mapped in the present study that are suitable for deployment in breeding programs towards increasing the yield of soybean. The inheritance of yield and yield-related traits reported here and the molecular markers linked to the mapped QTLs would be useful in a breeding program for enhancing the yield of soybean in the country.

Authors' contributions

Conceptualization of research (AT, RK); Designing of the experiments (AT, RK); Contribution of experimental materials (AT, SKL); Execution of field/lab experiments and data collection (RK, AT, PD, MS, DS); Analysis of data and interpretation (AT, RK, RP, KG, SKL); Preparation of the manuscript (AT, RK).

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