Theor Appl Genet (2003) 106:575–582
DOI 10.1007/s00122-002-1071-5

V.C. Concibido · B. La Vallee · P. Mclaird
N. Pineda · J. Meyer · L. Hummel · J. Yang · K. Wu
X. Delannay

Introgression of a quantitative trait locus for yield from *Glycine soja* into commercial soybean cultivars

Received: 20 March 2002 / Accepted: 17 June 2002 / Published online: 4 September 2002

Abstract The value of exotic germplasm in broadening the genetic base of most crops has been demonstrated many times. However, the difficulties involved in working with exotic germplasm have limited their utility in plant breeding. Unwanted linkages often thwart the successful incorporation of beneficial exotic genes into commercial lines. Thus, the use of exotics in traditional breeding makes the process of crop improvement a tedious, time-consuming and expensive endeavor. The availability of molecular markers makes it possible to isolate specific genomic regions and transfer them into commercial varieties with minimal linkage drag. We found a yield-enhancing quantitative trait locus (QTL) from *Glycine soja* (Siebold and Zucc.) by evaluating a population of 265 BC_2 individuals from a cross between HS-1 and PI 407305. The yield QTL was located on linkage group B2(U26) of the soybean [*Glycine max* (L.) Merrill] genetic linkage map. In a 2-year, multi-location study, individuals carrying the PI 407305 haplotype at the QTL locus demonstrated a 9.4% yield advantage over individuals that did not contain the exotic haplotype. When tested in a more uniform "HS-1-like" background in two locations, we observed an 8% yield advantage for lines that carry the PI 407305 haplotype. We further assessed the QTL effect in various elite soybean genetic backgrounds. The yield effect was consistently observed in only two of six genetic backgrounds. Individuals carrying the PI 407305 haplotype at the QTL locus had a 9% yield advantage in yield trials across locations. Despite the limited adaptability of this yield-QTL across genetic backgrounds, this study demonstrates the potential of exotic germplasm for yield enhancement in soybean.

Communicated by J.W. Snape

V.C. Concibido (✉) · B. La Vallee · P. Mclaird · N. Pineda
J. Meyer · L. Hummel · J. Yang · K. Wu · X. Delannay
Monsanto Co., 800 North Lindbergh Boulevard, St. Louis, MO 63167, USA
e-mail: Vergel.C.Concibido@monsanto.com
Tel.: +1314-694-1231, Fax: +1314-694-3914

Keywords Gene Mapping · *Glycine soja* · Exotic germplasm · Gene introgression · Genetic diversity · Yield enhancement

Introduction

Soybean [*Glycine max* (L.) Merrill], like most economically important crops, has a narrow genetic base. In fact, the North American soybean gene pool could be traced back to only 50 plant introductions with more than 80% of the northern and southern gene pool originating from less than a dozen introductions (Delannay et al. 1983; Gizlice et al. 1994). Like many other crops, the narrowing of soybean's genetic base has been brought about by decades of domestication and plant breeding. Since it was introduced in the U.S., soybean has achieved tremendous gains in yield through conventional breeding, largely due to hybridizations between elite soybean strains (Thorne and Fehr 1970). Ironically, that same process of plant breeding that accelerated genetic gain in soybean also led to the erosion of its genetic base.

The use of exotic germplasm offers a vast genetic resource that can broaden soybean's genetic base. In the past, breeders have tried to tap into the exotic germplasm to improve soybean and other crops with limited success, except in the case of disease resistance genes, where exotic germplasm had a major impact. This is due to the fact that beneficial genes, such as yield and seed quality traits, are complex and often trapped in tight genetic linkages with deleterious traits like lodging, seed shattering and susceptibility to pest and diseases. Furthermore, the use of wild germplasm in a breeding program requires several cycles of backcrossing to the adapted parent to recover most of the desirable agronomic traits, which can be costly, time-consuming, and is difficult to achieve while retaining the targeted allele from the exotic donor.

The availability of molecular markers has facilitated the identification, localization, and genetic dissection of loci that control quantitatively inherited traits, such as yield (Tanksley 1993). Molecular markers also offer a

faster and more accurate approach to breeding, since selection can now be based on genotype rather than solely on phenotype. Finally, molecular markers provide a way to successfully tap the genetic diversity available in exotic germplasm for crop improvement. Molecular markers now allow the isolation of beneficial genes that are often tied up in unfavorable linkages in exotic germplasm, and transfer into elite commercial germplasm (Tanksley and McCouch 1997).

In tomato, the concept of mining genes in wild relatives has been demonstrated successfully many times (Grandillo and Tanksley 1996; Tanksley et al. 1996, Fulton et al. 1997; Bernacchi et al. 1998; Monforte and Tanksley 2000). In rice, Xiao et al. (1998) found beneficial QTLs underlying important agronomic traits originating from *Oryza rufipogon*, a wild relative of cultivated rice, *Oryza sativa*.

In soybean, many of the beneficial genes that have been extracted from exotic or unadapted germplasm using molecular markers are involved in pest and disease resistance. Examples of QTLs for pest resistance from exotic germplasm include soybean cyst nematode, SCN (Concibido et al. 1994; Webb et al. 1995, Concibido et al. 1997), peanut root-knot nematode (Tamulonis et al. 1997), and corn earworm (Rector et al. 2000; Terry et al. 2000). For disease resistance, QTLs from exotic soybean relatives have been reported for brown stem rot (Klos et al. 2000), soybean mosaic virus (Hayes et al. 2000) and Phytophthora root rot (Hegstad et al. 1998). Other studies resulted in the discovery of QTLs for oil, protein and other seed quality traits (Diers et al. 1992; Lark et al. 1994; Brummer et al. 1997; Sebolt et al. 2000). The search for yield QTLs originating from exotic germplasm is not a new concept in soybean (Lark et al. 1995; Maughan et al. 1996; Mian et al. 1996; Orf et al. 1999a, b). However, none of these studies addressed the issue of adaptability of exotic yield QTLs across genetic backgrounds.

Here, we report the identification, localization, and validation in elite genetic backgrounds of a yield-enhancing QTL in soybean that was derived from a wild *Glycine soja* (Siebold & Zucc.) accession, PI 407305.

Materials and methods

Mapping populations

The development of the two mapping populations used in this study is shown in Fig. 1. The first is a BC_2F_1 and the other is an F_2, both from the cross between soybean line HS-1 (Jacob Hartz Seed, Stuttgart, Arkansas, USA) and *G. soja* accession PI 407305 (United States Department of Agriculture Soybean Germplasm Collection, University of Illinois, Urbana-Champaign, USA). PI 407305 is a wild annual, procumbent, maturity group V, soybean with tiny black seeds that originated from Southern China. HS-1 is a high stearate soybean line developed by Jacob Hartz Seed from the cross between A6, a high stearate soybean line, and Hartz variety H5668. First, a cross was made between HS-1 and PI 407305. The resulting F_1 progeny was backcrossed twice to the adapted parent line, HS-1. There were 40 BC_1F_1 progenies used to generate 265 BC_2F_1 individuals. On average, the BC_2F_1 population consisted of about seven BC_2F_1 progenies from each of the 40 BC_1F_1 progenitor lines. The most represented BC_1F_1 progenitor line contributed 17 BC_2F_1 progenies and the least represented BC_1F_1 progenitor line had one BC_2F_1 progeny. The BC_2F_1 individuals were grown and leaf tissues were collected for DNA analysis.

The F_2 mapping population was developed to anchor our BC_2F_1 linkage map with the public soybean genetic linkage map (Cregan et al. 1999). Two F_1 plants were selfed to generate 96 F_2 individuals. The F_2 progenies were grown and leaf tissues were taken for DNA marker analysis.

Backcross-derived sibling line development

To test the QTL effect in a more uniform "HS-1-like" genetic background, a single BC_2F_3 plant derived from the HS-1 × PI 407305 BC_2F_1 population, heterozygous for all the markers spanning the QTL region, was selfed (Fig. 1). The resulting progenies were then space-planted and genotyped for selected markers around the yield QTL region. Twenty five plants were identified from each of two classes: those that were homozygous for the PI 407305 haplotype and those that were homozygous for the HS-1 haplotype for the selected markers around the yield QTL region. Seeds of each of the homozygous classes were bulked and used in yield tests across two locations in 1998. To test the QTL effect in other elite genetic backgrounds, BC_1-lines were developed using six Asgrow lines (AG4501, AG2401, QR4459, QP4459, QR4544 and QP4604) (Fig. 1). First, each of the elite Asgrow line was backcrossed to a BC_2F_4 plant derived from the original HS-1 × PI 407305 BC_2F_1 mapping population that was homozygous for the PI 407305 haplotype markers spanning the putative yield QTL. Another cycle of backcrossing was performed on AG4501 to generate BC_2 near-isogenic lines (see Fig. 1). Again, molecular markers were used to identify and bulk-harvest the plants that were homozygous for the PI 407305 haplotype at the QTL locus and plants that were homozygous for the non-PI 407305 haplotype at the QTL locus for each of the six elite lines. On average, 25 plants each were bulked for the contrasting isogenic pairs.

QTL mapping and validation strategy

The strategy that we used to identify and validate yield-enhancing QTLs from exotic soybean was divided in three stages. The first stage (QTL discovery) involves the identification of exotic genomic regions associated with increased yield in the BC_2F_1 population. The second stage involves the validation of QTL effect in a more uniform "HS-1-like" background. The third stage involves the confirmation of the yield effect in six additional elite soybean genetic backgrounds to assess the QTL's commercial potential. We also assessed the novelty and frequency of the putative exotic yield QTL by comparing the haplotype of the exotic donor, PI 407305, at the QTL region with the haplotypes of various soybean germplasm including commercial varieties and exotic plant introductions.

Experimental design

The BC_2F_1 QTL discovery (Stage 1) population was planted in three locations in 1996 and seven locations in 1997 (Fig. 1). The second stage QTL validation study, which was aimed at evaluating the QTL effect in a more uniform "HS-1 like" background, was planted in a randomized complete block design (RCBD) with four replications in 1998 across two locations (Fig. 1). The third stage QTL validation study on six elite soybean backgrounds was conducted using RCBD in the summer of 2000 (Fig. 1). The AG4501 BC_2-and AG2401 BC_1-derived lines were tested in five locations and two replications. While the QR4459, QP4459, QR4544 and QP4604, BC_1-derived lines, were tested in only one location with two replications. Plots were harvested with a combine to measure seed yield. At harvest, only the test rows were harvested and seed yield was adjusted to 13% moisture content to derive the dry yield for each line in kg ha^{-1}.

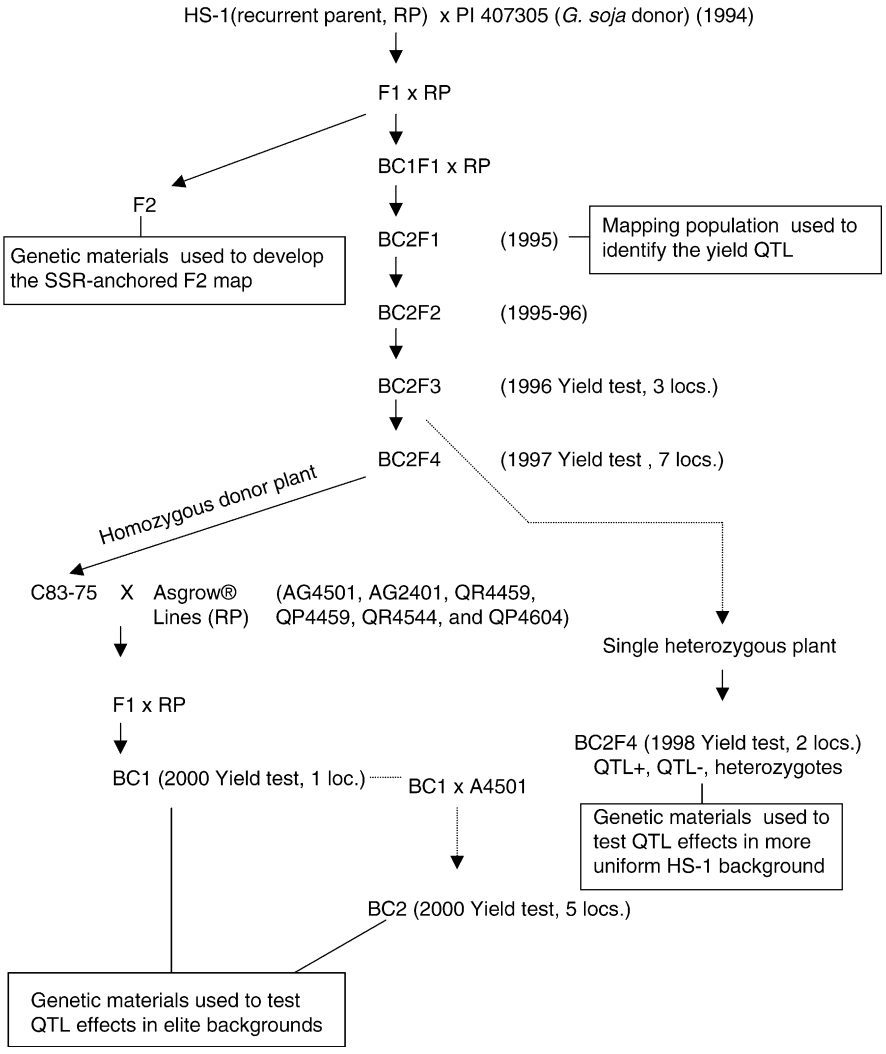

Fig. 1 Flow chart showing the development of the test populations used in the study

Agronomic practices

Cultural practices, such as herbicide applications and fertilization, were carried out following the standard recommendations for soybean. Plant height, maturity, shattering, and lodging were recorded and used to determine the independence of the yield QTL from any deleterious traits. Other agronomic traits were also measured including growth habit, seed coat color and pod color.

DNA analysis and QTL mapping

AFLP genotyping was performed as described by Vos et al. (1995). A BC_2F_1 genetic map was generated using Mapmaker (Lander et al. 1987). Linkage between AFLP markers was inferred whenever the LOD score was 2.0 or higher. To locate putative yield-enhancing QTLs, significant associations between marker loci and yield were determined at $P = 0.001$ using QGene (Nelson 1997) and SAS (SAS Institute 1987) in each of the test environments. A combined analysis of the data from all ten environments was performed using one-way analysis of variance (ANOVA) employing SAS (SAS Institute 1987) with a marker genotype (classified as presence and absence of the exotic yield haplotype, QTL+/QTL–) as treatment and the ten locations as replications in the model. We also assessed the independence of the putative yield QTL effects from deleterious traits such as lodging, maturity and shattering.

A second map was constructed using an F_2 population of the same cross, HS-1 × PI 407305, consisting of 96 individuals. Using Mapmaker, we built a map with 600 SSR markers. SSR genotyping was performed as described by Cregan et al. (1999). Linkage between SSR markers was inferred whenever the LOD score was 2.0 or higher.

Results

Map construction and linkage analysis

Initially, we tried to build a linkage map using the BC_2F_1 population consisting of 265 individuals with 212 AFLPs and four morphological markers (seed coat color, *i*; determinate stem, dt_1; and pod color, l_1, and l_2). AFLP technology was used since it was the genotyping platform in Monsanto when the study was initiated.

As SSRs became available, it was imperative to incorporate SSR markers on our map to anchor it to the public soybean genetic linkage map (Cregan et al. 1999). With the inherent problems associated with map development using the BC_2F_1 population, and the dominant nature of AFLP markers, it became apparent that the BC_2F_1 map was not informative enough and less useful due to the

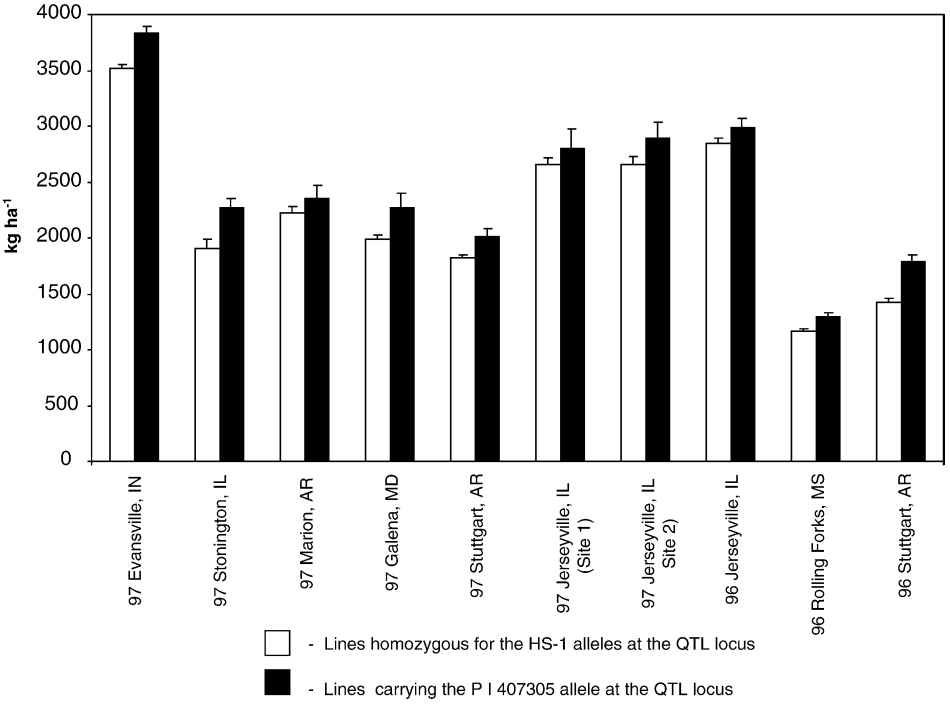

Fig. 2 Mean yields of BC_2F_1 lines carrying the *G. soja*, PI 407305, allele at the AFLP marker U3944 locus compared to BC_2F_1 lines homozygous for the HS-1 allele at the AFLP marker U3944 locus across years and locations

lack of 'anchor' markers (markers known to map on specific linkage groups on the soybean genetic linkage map) that can link it to the public soybean genetic linkage map (Cregan et al. 1999). In addition, the limited amount of remnant DNA from our BC_2F_1 population made it impossible to place the more than 600 SSR markers that became available later in the course of the study. For these reasons, the HS-1 × PI 407305 F_2 mapping population was developed to anchor our AFLP map with the public soybean genetic linkage map.

We localized our putative yield QTL on linkage group B2(U26) of the soybean genetic linkage map (Cregan et al. 1999) by placing AFLP markers spanning the yield QTL onto the F_2 SSR map. In the process, we were able to identify several SSR markers that might be associated with the yield QTL originating from the *G. soja* accession, PI 407305, by virtue of their linkage to AFLP markers spanning the yield QTL. We immediately performed QTL analysis on the BC_2F_1 population using the newly found SSR markers and confirmed that the yield QTL lies on linkage group B2(U26), flanked by Satt560 and Satt168 (Table 1). Interval-mapping analysis (Lander and Botstein 1989) results showed that the most significant marker, Satt066, has a peak LOD score of 3.67 (Table 1).

Initially, AFLP marker U3944 was the most significant marker in the region and was used to monitor the presence or absence of the PI 407305 haplotype in our BC-derived sibling lines for the subsequent QTL validation studies (Stages 2–3). Since AFLP U3944 is a dominant marker, it did not allow us to distinguish the homozygous from the heterozygous lines. This required an additional progeny test in developing our BC-derived sibling lines. We attempted, but failed, to develop co-dominant PCR-based markers from the AFLP band associated with the yield QTL locus.

The discovery of SSR markers tightly linked to the yield QTL locus allowed us to monitor the positive introgression of the yield QTL more easily and eliminated the need for progeny testing. Currently, we have 12 SSRs around the genomic region associated with the yield increase contributed by PI 407305 (Table 1).

QTL discovery in HS-1 × PI 407305

Figure 2 shows bar graphs representing mean yield contrasts of heterozygous and homozygous BC_2F_1 lines for the alleles at the ALFP marker U3944 locus across locations in 1996 and 1997. Six out of ten locations show significant yield increases in BC_2F_1 lines carrying the PI 407305 alleles at the AFLP marker U3944 locus as compared to BC_2F_1 lines homozygous for the HS-1 alleles at the same locus (Fig. 2, Table 2). Heterozygous BC_2F_1 lines, containing the PI 407305 allele, had a significantly higher seed yield (12% on average across locations) compared to BC_2F_1 lines that were homozygous for the HS-1 haplotype (Table 2). A combined analysis of data across test environments showed a 9.3% ($P < 0.0001$) yield increase of lines carrying the PI 407305 alleles for the markers around the yield QTL locus over lines carrying the alleles for HS-1 (Tables 2–3).

To determine the presence of the PI 407305 haplotype in other soybean germplasm, we surveyed over 70 lines including wild and commercial soybean varieties with SSR markers spanning the QTL region (Table 4). Our results showed that the *G. soja* haplotype is unique to PI 407305 (Fig. 3). We are aware that we have tested a limited number of soybean lines, but the narrow genetic base available in present commercial soybean varieties

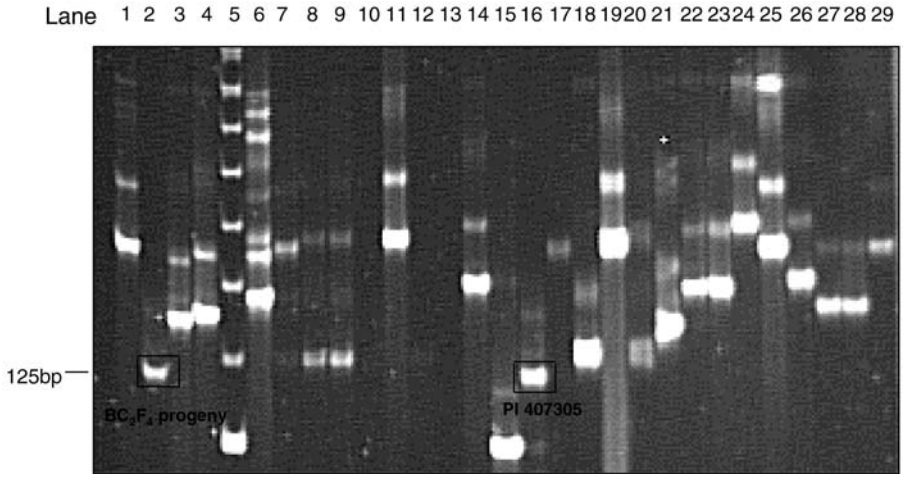

Fig. 3 Gel image of soybean lines analyzed with Satt534 on linkage group B(U26) showing the uniqueness of the yield-QTL allele (147-bp fragment) originating from *G. soja*, PI 407305, accession. Among the 70 soybean lines evaluated (28 lines shown), including plant introductions and commercial varieties, only a BC_2F_4 progeny line (*lane 2*) from the HS-1 × PI 407305 BC_2F_1 mapping population, which was used as a positive check in this gel, shares the Satt534 allele with PI 407305 (*lane 16*). lane 5 is a 25-bp DNA ladder and lanes 10, 12 and 13 are missing

Table 1 Interval analysis of linkage group B2(U26) spanning the genomic region around the yield-QTL derived from *G. soja* accession, PI 4070305, from the HS-1 × PI 407305 BC_2F_1 mapping population across locations in 1996 and 1997

Marker	Map position (cM)	Number of lines	*F*-value	*P*-value	LOD[a]
Satt560	0.0	244	3.69	0.0559	1.90
Satt534	8.1	246	7.83	0.0055	3.51
Satt066	12.6	240	15.34	0.0001	3.67
AFLPU3944	15.0	248	15.46	0.0001	2.85
Satt020	15.8	237	18.25	<0.0001	2.49
Satt272	15.8	250	16.58	0.0001	2.49
Sct_094	16.8	223	18.12	<0.0001	2.15
Satt556	17.3	240	13.97	0.0002	2.14
Satt122	17.3	253	13.76	0.0003	2.14
Satt474	17.3	256	14.01	0.0002	2.14
Sat_083	17.3	242	6.77	0.0098	2.14
Satt416	21.8	243	8.86	0.0032	1.66
Satt168	24.7	247	7.52	0.0066	1.16

[a] LOD-$\log_{10}$ of the odds ratio, a QTL is inferred whenever the LOD score exceeded the threshold of 2.0

Table 2 Average percent yield increases attributed to the yield QTL from *G. soja* accession, PI 407305, across years and locations in contrasts between heterozygous BC_2F_1 lines carrying the *G. soja* haplotype at the QTL locus compared to BC_2F_1 lines homozygous for the HS-1 haplotype at the QTL locus

Location	Year	Percent yield increase	*P*-value
Jerseyville, IL	1996	5.0	0.2085
Rolling Forks, MS	1996	10.3	0.0307
Stuttgart, AR	1996	26.1	<0.0001
Evansville, IN	1997	9.0	0.0012
Galena, MD	1997	14.6	0.0124
Jerseyville, IL (site 1)	1997	5.3	0.3774
Jerseyville, IL (site 2)	1997	8.6	0.1970
Marion, AR	1997	6.0	0.3145
Stonington, IL	1997	19.0	0.0474
Stuttgart, AR	1997	10.7	0.0145
Combined Years and Locations		9.4	<0.0001

Table 3 Analysis of variance for the combined data from all test environments involving BC_2F_1 lines carrying the *G. soja* haplotype for the markers around the QTL locus compared to BC_2F_1 lines homozygous for the HS-1 haplotype for the markers around the QTL locus with locations used as replications

Source	*df*	Sum of squares	Mean square	*F*-value	*P*-value
Rep	9	9,011,298.812	1,001,255.424	209.38	<0.0001
Genotype	1	264,086.162	264,086.162	55.23	<0.0001
R-Square		0.995381			
CV		2.962134			

increases the likelihood that this particular haplotype from PI 407305 is not present in the current soybean germplasm base.

QTL validation in a more uniform "HS-1-likes" background

To validate the QTL effects found in PI 407305 in a more uniform "HS-1-like" background, we developed BC_2-derived siblings differing primarily in the presence or absence of the PI 407305 haplotype based on SSR markers spanning the QTL region. One out of two locations showed significant differences with lines homozygous for the PI 407305 haplotype with more than a 18% yield increase over lines homozygous for the HS-1 haplotype (Table 5). Also, the yield effect contributed by the *G. soja* parent appeared to be dominant (Table 5).

Besides increased yield, other phenotypic differences attributable to the presence of the PI 407305 haplotype were observed. Lines that were homozygous for the PI 407305 haplotype at the QTL locus showed a significant increase in plant height compared to lines that were homozygous for the HS-1 haplotype (Table 5). It can be inferred that increased height can translate to increased internode number and increased pod number per plant, thus to increased yield. With this in mind, we also counted the number of pods on the main stem. Five plants each from lines homozygous for the PI 407305 haplotype, heterozygous or homozygous for the HS-1 haplotype at the yield QTL locus were used to assess differences in the number of pods on the main stem. However, we did not see any significant differences (Table 5).

We also mapped other traits that might have contributed to the yield increase associated with the PI 407305 haplotype. Lodging, shattering and maturity were rated during the QTL discovery and validation stages (data not shown). None of these traits was linked to the yield QTL contributed by the *G. soja* accession, PI 407305.

Table 4 Lists of soybean lines evaluated for the presence of the PI 407305 haplotype associated with yield increase using SSR markers flanking the QTL region

Entry			
A0868	C83-75	HLL	PI 323550
A1900	Cristallina	HS-1	PI 326581
A2247	CX445	HS2	PI 339732
A2553	FPG2975	Jack	PI 342621C
A2701	FT108	Minsoy	PI 360843
A2702	H3090RR	Noir-1	PI 366120
A2883	H4994RR	PI 153292	PI 371610
A3002	H4998RR	PI 153296	PI 371611
A3244	H5050	PI 159764	PI 398620
AG3302	H5181RR	PI 165583	PI 407922
AG5401	H6255	PI 196504	PI 423871
AG5545	H632A	PI 200508	PI 428692
Archer	H632A	PI 205090	PI 437088B
B2W	H635B	PI 208438	PI 468916
BPG4878	H635B	PI 208439	PI 548399
C113	H638C	PI 261469	PI 548608
C1944	H6397	PI 291281	PI 891549
C1945	H7152	PI 291309B	PI 159926

Table 5 Mean yield, plant height (cm) and number of pods at the main stem at maturity of near-isogenic populations derived from HS-1 × PI 407305 BC_2F_1 mapping population differing primarily due to the presence or absence of the *G. soja* alleles for the markers around the QTL locus. Means followed by the same letter are not significantly different from each other at $P \leq 0.05$ (Duncan Multiple Range Test)

Haplotype at the yield-QTL locus	Yield (kg ha^{-1})	Plant height (cm)	Pods at main stem
Homozygous for PI 407305	2997.1^{A}	65.4^{A}	41.9^{A}
Heterozygous	2909.8^{A}	64.9^{AB}	40.5^{A}
Homozygous for HS-1	2526.7^{B}	58.9^{B}	30.5^{A}

QTL validation in elite genetic background

To assess the adaptability of the *G. soja* yield-QTL across genetic backgrounds, we developed sibling lines derived from BC_1 and BC_2 populations in the following Asgrow germplasm: AG4501, AG2401, QR4459, QP4459, QR4544 and QP4604. Table 6 shows that the efficacy of the yield QTL was limited to AG4501 and QP4459. Lines that were homozygous for the PI 407305 haplotype at the QTL locus demonstrated a 9% yield increase ($P = 0.0006$) over lines that were homozygous for the AG4501 haplotype (Table 6). In the QP4459 background, the presence of the PI 407305 haplotype showed a 5% yield increase ($P = 0.0119$) over lines that were homozygous for the

Table 6 Efficacy of the yield-QTL derived from *G. soja* accession, PI 4070305, across genetic backgrounds based on bulk isogenic lines differing primarily due to the presence or absence of the *G. soja* haplotype for the markers around the QTL locus at the QTL locus

Genetic background	Year tested	Total locations	QTL positive (kg ha^{-1})	QTL negative (kg ha^{-1})	Percent yield increase	CV (%)	*P*-value
HS-1	1998	2	2,808.9	2,607.4	7.7	17.8	0.0054
AG4501	2000	5	1,559.0	1,431.4	8.9	6.3	0.0006
AG2401	2000	5	2,016.0	1,888.3	6.7	30.0	0.1057
QP4459	2000	1	2,002.6	1,908.5	4.9	6.2	0.0119
QR4459	2000	1	2,116.8	2,157.1	–1.9	6.7	0.7148
QR4544	2000	1	2,089.9	2,136.9	–2.2	10.2	0.6541
QR4604	2000	1	2,029.4	2,076.5	–2.3	10.1	0.5210

QP4459 haplotype (Table 6). None of the other genetic backgrounds showed any significant differences between lines carrying the PI 407305 haplotype and lines carrying the elite haplotype for the QTL locus.

Discussion

Despite soybean's narrow genetic base, the use of exotic germplasm has not been fully exploited in conventional soybean breeding programs largely due to the success of breeders in crossing elite × elite strains to generate superior cultivars (Thorne and Fehr 1970). Thorne and Fehr (1970) further stated that two- and three-way crosses involving at least one unadapted parent have a low frequency of superior segregates in their progeny. The limited opportunity for genetic recombination in two- or three-way crosses and the paucity of adequate evaluation of the yield potential of the unadapted parent germplasm further contributed to the lack of success in breeding with exotic germplasm in the past (Schoener and Fehr 1979).

With the availability of molecular markers and the existence of programs like SAGE (Soybean Asian Germplasm Evaluation), the use of exotic germplasm is more attractive than before. Molecular markers allow the delivery of beneficial genes from the wild into commercial varieties with a tolerable amount of linkage drag. Furthermore, the judicious selection of exotic parents, as a result of collaborative efforts among soybean researchers in assessing the utility of soybean plant introductions through the SAGE program, can improve the likelihood of finding beneficial genes in the wild or unadapted germplasm.

Despite the limited adaptability across genetic backgrounds of the yield-QTL found in this study, our results clearly demonstrate the potential of using exotic germplasm to improve soybean yield. We only evaluated the QTL extensively in two genetic backgrounds (AG4501 and AG2401), thus it is still possible that this QTL might be useful in other genetic backgrounds similar to that of AG4501.

The availability of a number of SSR markers around the QTL region makes it a good candidate for marker-assisted breeding and can serve as good starting points for map-based cloning.

Acknowledgements We thank Dr. Alan Walker and the Monsanto Global Soybean Seed Group for field-testing the plant materials used in the study. We also thank Dr. Marlin Edwards, Dr. Brian Diers and Dr. Prakash Arelli for their critical review of the manuscript. Seeds of the progenies of the test population were deposited in the American Type Culture Collection (ATCC, 10801 University Blvd., Manasas, VA 20110-2209, USA) on May 6, 1998, and designated as ATCC 203138, 203139, 203140. Asgrow and Hartz are registered trademarks of Monsanto Company.

References

Bernacchi D, Beck-Bunn T, Eshed Y, Lopez J, Petiard V, Uhlig J, Zamir D, Tanksley S (1998) Advanced backcross QTL analysis in tomato. I. Identification of QTLs for traits of agronomic importance from *Lycopersicon hirsutum*. Theor Appl Genet 97:381–397

Brummer EC, Graef GL, Orf J, Wilcox JR, Shoemaker RC (1997) Mapping QTLs for seed protein and oil content in eight soybean populations. Crop Sci 37:370–378

Concibido VC, Denny RL, Boutin SR, Hautea R, Orf JH, Young ND (1994) DNA marker analysis of loci underlying resistance to soybean cyst nematode (*Heterodera glycyines* Ichinohe). Crop Sci 314:240–246

Concibido VC, Denny R, Lange D, Danesh D, Orf J Young N (1997) Genome mapping of soybean cyst nematode resistance genes in 'Peking', PI 90763, and PI 88788 using DNA markers. Crop Sci 37:258–264

Cregan PB, Jarvik T, Bush AL, Shoemaker RC, Lark KG, Kahler AL, VanToai TT, Lohnes DG, Chung J, Specht JE (1999) An integrated genetic linkage map of the soybean genome. Crop Sci 39:1464–1490

Delannay X, Rodgers DM, Palmer RG (1983) Relative genetic contributions among ancestral lines to North American soybean cultivars. Crop Sci 23:944–949

Diers BW, Keim P, Fehr WR, Shoemaker RC (1992) RFLP analysis of soybean seed protein and oil content. Theor Appl Genet 83:608–612

Fulton TM, Nelson JC, Tanksley SD (1997) Introgression and DNA marker analysis of *Lycopersicon peruvianum* a wild relative of the cultivated tomato into *Lycopersicon esculentum* followed through three successive backcross generations. Theor Appl Genet 95:895–902

Gizlice Z, Carter TE Jr, Burton JW (1994) Genetic base for North American public soybean cultivars released between 1947 and 1988. Crop Sci 34:1143–1151

Grandillo S, Tanksley SD (1996) QTL analysis of horticultural traits differentiating the cultivated tomato from the closely related species *Lycopersicon pimpinellifolium*. Theor Appl Genet 92:935–951

Hayes AJ, Ma G, Buss GR, Saghai Maroof MA (2000) Molecular marker mapping of a *RSV4* gene conferring resistance to all known strains of soybean mosaic virus. Crop Sci 40:1434–1437

Hegstad JM, Nickell CD, Vodkin LO (1998) Identifying resistance to *Phytophthora sojae* in selected soybean accessions using RFLP techniques. Crop Sci 38:50–55

Klos KLE, Paz MM, Fredrick Marek L, Cregan PB, Shoemaker RC (2000) Molecular markers useful for detecting resistance to brown stem rot. Crop Sci 40:1445–1452

Lander ES, Botstein D (1989) Mapping Mendelian factors underlying quantitative traits using RFLP linkage maps. Genetics 121:185–189

Lander ES, Green P, Abrahamson J, Barlow A, Daly MJ, Lincoln SE (1987) Mapmaker: an interactive computer package for constructing genetic linkage maps of experimental and natural populations. Genomics 1:174–181

Lark KG, Orf J, Mansur LM (1994) Epistatic expression of quantitative trait loci (QTL) in soybean [*Glycine max* (L.)] determined by QTL association with RFLP alleles. Theor Appl Genet 88:486–489

Lark KG, Chase K, Adler F, Mansur LM, Orf JH (1995) Interactions between quantitative trait loci in soybean in which trait variation at one locus is conditional upon a specific allele at another. Proc Natl Acad Sci USA 92:4656–4660

Maughan PJ, Saghai Maroof MA, Buss GR (1996) Molecular-marker analysis of seed-weight: genomic locations gene action and evidence for orthologous evolution among three legume species. Theor Appl Genet 93:574–579

Mian MAR, Bailey MA, Tamulonis JP, Shipe ER, Carter TE Jr, Parrott WA, Ashely DA, Hussey RS, Boerma HR (1996) Molecular markers associated with seed weight in two soybean populations. Theor Appl Genet 93:1011–1016

Monforte AJ, Tanksley SD (2000) Fine mapping of a quantitative trait locus (QTL) from *Lycopersicon hirsutum* chromosome 1 affecting fruit characteristics and agronomic traits: breaking linkage among QTLs affecting different traits and dissection of heterosis for yield. Theor Appl Genet 100:471–479

Nelson JC (1997) QGene: software for marker-based genomic analysis and breeding. Mol Breed 3:229–235

Orf JH, Chase K, Jarvik T, Mansur LM, Cregan PB, Adler FR, Lark KG (1999a) Genetics of soybean agronomic traits. I. Comparison of three related recombinant inbred populations. Crop Sci 39:1642–1651

Orf JH, Chase K, Adler FR, Mansur LM, Lark KG (1999b) Genetics of soybean agronomic traits. II. Interactions between yield quantitative trait loci in soybean. Crop Sci 39:1652–1656

Rector BG, All JN, Parrott WA, Boerma HR (2000) Quantitative trait loci for antibiosis resistance to corn earworm in soybean. Crop Sci 40:233–238

SAS Institute (1987) SAS/STAT guide for personal computers Version 6 edn. SAS Institute, Cary, North Carolina

Sebolt AM, Shoemaker RC, Diers BW (2000) Analysis of a quantitative trait locus allele from wild soybean that increases seed protein concentration in soybean. Crop Sci 40:1438–1444

Schoener CS, Fehr WR (1979) Utilization of plant introductions in soybean breeding populations. Crop Sci 19:185–188

Tamulonis JP, Luzzi BM, Hussey RS, Parrott WA, Boerma HR (1997) DNA marker analysis of loci conferring resistance to peanut root-knot nematode in soybean. Crop Sci 95:664–67

Tanksley SD (1993) Mapping polygenes. Annu Rev Genet 27:205–233

Tanksley SD, McCouch SR (1997) Seed banks and molecular maps: unlocking genetic potential from the wild. Science 277:1063–1066

Tanksley SD, Grandillo S, Fulton T, Zamir D, Eshed T, Petiard V, Lopez J, Beck-Bunn T (1996) Advanced backcross QTL analysis in a cross between an elite processing line of tomato and its wild relative *L. pimpinellifolium*. Theor Appl Genet 213–224

Terry LI, Chase K, Jarvik T, Orf J, Mansur L, Lark KG (2000) Soybean quantitative trait loci for resistance to insects. Crop Sci 40:375–382

Thorne JC, Fehr WR (1970) Exotic germplasm for yield improvement in two-way and three-way soybean crosses. Crop Sci 10:677–678

Vos P, Hogers R, Bleeker M, Reijans M, van de Lee T, Hornes M, Frijters A, Pot J, Peleman J, Kulper M, Zabeau M (1995) AFLP: a new technique for DNA fingerprinting. Nucleic Acids Res 23:4407–4414

Webb DM, Baltazar BM, Rao-Arelli AP, Schupp J, Clayton K, Keim P, Beavis WD (1995) Genetic mapping of soybean cyst nematode race-3 resistance loci in soybean PI437.654. Theor Appl Genet 91:574–581

Xiao J, Li J, Grandillo S, Yuan L, Tanksley SD, McCouch SR (1998) Identification of trait-improving quantitative trait loci alleles from a wild rice relative*Oryza rufipogon*. Genetics 150:899–909