Seed Yield of Near-Isogenic Soybean Lines with Introgressed Quantitative Trait Loci Conditioning Resistance to Corn Earworm (Lepidoptera: Noctuidae) and Soybean Looper (Lepidoptera: Noctuidae) from PI 229358

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ABSTRACT The development of superior soybean, *Glycine max* (L.) Merr., cultivars exhibiting resistance to insects has been hindered due to linkage drag, a common phenomenon when introgressing alleles from exotic germplasm. Simple-sequence repeat (SSR) markers were used previously to map soybean insect resistance (SIR) quantitative trait loci (QTLs) in a 'Cobb' × PI 229358 population, and subsequently used to create near-isogenic lines (NILs) with SIR QTL in a 'Benning' genetic background. SIR QTLs were mapped on linkage groups (LGs) M (SIRQTL-M), G (SIRQTL-G), and H (SIRQTL-H). The objectives of this study were to 1) evaluate linkage drag for seed yield by using Benning-derived NILs selected for SIRQTL-M, SIRQTL-H, and SIRQTL-G; 2) assess the amount of PI 229358 genome surrounding the SIR QTL in each Benning NIL; and 3) evaluate the individual effects these three QTLs on antibiosis and antixenosis to corn earworm, *Helicoverpa zea* (Boddie), and soybean looper, *Pseudoplusia includens* (Walker). Yield data collected in five environments indicated that a significant yield reduction is associated with SIRQTL-G compared with NILs without SIR QTL. Overall, there was no yield reduction associated with SIRQTL-M or SIRQTL-H. A significant antixenosis and antibiosis effect was detected for SIRQTL-M in insect feeding assays, with no effect detected in antixenosis or antibiosis assays for SIRQTL-G or SIRQTL-H without the presence of PI 229358 alleles at SIRQTL-M. These results support recent findings concerning these loci.

KEY WORDS corn earworm, *Glycine max*, marker-assisted selection, quantitative trait loci, soybean looper

Increased soybean, *Glycine max* (L.) Merr., production in the southern United States over the past half-century prompted development of integrated pest management programs aimed at limiting yield losses from a host of insect pests. The subtropical climate conditions and long growing seasons of this region make soybean especially vulnerable to economic losses resulting from insect infestations (Boethel 1999). Pesticide applications have been the primary control method used when insect infestations reach threshold levels. Such chemical control measures are economically unattractive to growers due to soybean's low value per hectare in the southeastern United States (Boethel 1999). Moreover, the detrimental environmental impacts created by repeated pesticide use in agricultural production systems have been well documented for some time (Boethel 2004). Soybean insect resistance (SIR) can be a management tactic compatible with, and a supplement to, threshold-triggered insecticide applications.

The major sources of insect resistance germplasm used in U.S. soybean breeding programs to this point have been three Japanese plant introductions (PIs): PI 171451 ('Kosamame'), PI 229358 ('Soden-daizu'), and PI 227687 ('Miyako White'). Because these PIs exhibit resistance to nearly all major soybean defoliators, they have served as the primary donor parents in breeding for resistance to multiple insects (Clark et al. 1972; Hatchett et al. 1976; Lambert and Kilen 1984; Van Duyn et al. 1971, 1972). The types of plant resistance to insects have been described previously (Painter 1951, Kogan and Ortman 1978, Lambert and Kilen 1984) and include antixenosis and antibiosis. Although antixenosis and antibiosis are each described as distinct resistance modalities, they are not mutually exclusive (Painter 1951; Rector et al. 1999, 2000). Antixenosis, also known as nonpreference, encompasses any biochemical or morphological trait that discourages or repels insect feeding, oviposition, or colonization (Painter 1951, Kogan and Ortman 1978). Antibiosis refers to any detrimental physiological effect on insect development, growth, and/or reproduction caused by feeding on plant tissue.

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Soybean resistance to insect defoliation is a quantitative trait. The use of molecular markers in quantitative trait loci (QTLs) mapping has made it feasible to evaluate the relative phenotypic variation associated with discrete SIR loci (Boerma and Mian 1999). Rector et al. (1998, 1999, 2000) used restriction fragment length polymorphism (RFLP) markers to map QTLs associated with antixenosis and antibiosis resistance to corn earworm, *Helicoverpa zea* (Boddie), in three individual crosses of the susceptible 'Cobb', to the three SIR PIs, PI 171451, PI 227687, and PI 229358. A major SIR QTL with its resistance allele contributed from PI 229358 was detected on linkage group (LG) M (SIR-M) for both antixenosis (R^2 = 37%) and antibiosis (R^2 = 22%), whereas two QTLs with smaller effects were identified on LG G (SIR-G) and LG H (SIR-H) for antibiosis (R^2 = 19%) and antixenosis (R^2 = 16%), respectively. In a follow-up study, the SIR QTLs were mapped using SSR markers in the Cobb × PI 229358 population, which provided more precise estimates of QTL locations on each linkage group (Narvel et al. 2001).

Although U.S. soybean breeders and entomologists have developed numerous SIR breeding lines and released four SIR cultivars, none have been widely used by soybean producers, primarily due to their low yield potential or lower insect resistance than the donor parent (Narvel et al. 2001). Success in producing high-yielding, agronomically acceptable SIR cultivars may hinge upon continued advances in molecular biology, as well as in efforts by researchers to elucidate the most efficient and cost-effective breeding techniques for SIR. The phenomenon of linkage drag has been implicated as a cause of the limited success in developing high-yielding cultivars with endogenous insect resistance (Boethel 1999; Sisson et al. 1976, Rufener et al. 1989).

Marker-assisted selection (MAS) has been used in modern breeding programs as an alternative or supplement to phenotypic selection. Narvel et al. (2001) used SSR markers to determine the success of phenotypic selection for insect resistance by assessing how many of the known SIR QTLs were present in each of 15 advanced SIR genotypes and the amount of donor PI 229358 genome introgressed along with SIR-M. Although the SIR-M had been introgressed into most lines, it was evident that phenotypic selection had been unsuccessful in transferring SIR-G and SIR-H into most of the advanced germplasms, which would explain why they have lower levels of resistance than the donor parent. More importantly, phenotypic selection had maintained major segments of the donor genome surrounding the major SIR-M in many of the advanced breeding lines and cultivars.

Near-isogenic lines (NILs) derived from Benning (7) × PI 229358 were developed using MAS before each backcross (six backcrosses) with Benning (Zhu et al. 2006). These NILs provide the unique opportunity to study the effects of individual SIR QTLs within an elite genetic background and assess the effectiveness of MAS in breeding for superior SIR cultivars.

The objectives of this study were 1) to evaluate linkage drag associated with seed yield by using Benning-derived NILs selected for SIR-M, SIR-H, and SIR-G; 2) to assess the amount of PI 229358 genome surrounding each SIR QTL in each Benning NIL; and 3) to evaluate the individual effects these three QTLs on antibiosis and antixenosis to soybean looper, *Pseudoplusia includens* Walker, and corn earworm.

Materials and Methods

The 2004 tests used BC_6F_2-derived NILs in a Benning background (Zhu et al. 2006), which were developed by selecting plants based on individual SSR genotypes at previously determined SIR QTLs and through phenotypic screening for antixenosis and antibiosis resistance. Benning is a maturity group VII cultivar that is adapted to the southeastern United States (Boerma et al. 1997). Concurrently, five lines also were selected for homozygous Benning alleles at SIR-M, SIR-H, and SIR-G concurrently, thus creating a set of control lines.

In 2005, two BC_6F_2-derived lines representing SIR-M, SIR-H, and SIR-G were chosen based on their overall agronomic performance and similarity to Benning in 2004. Also, included in 2005 were three entries of the Benning cultivar and three lines homozygous for PI 229358 alleles at all three SIR QTLs. For simplicity, the NILs will henceforth be referred to as Benning-M, Benning-H, and Benning-G, Benning-mgh (control lines lacking the three SIR alleles), and Benning-MGH (all three SIR alleles combined in one NIL).

To evaluate seed yield of individual SIR genotypes, the NILs were grown in two trials at the University of Georgia Plant Sciences Farm near Watkinsville, GA, and in one trial at the University of Georgia Southwest Research and Education Center near Plains, GA. The trials were planted on 21 May 2004 and 18 June 2004 at the Plant Sciences Farm and on 14 May 2004 at Plains. Each experiment was arranged in a randomized complete block with three replications. 25 entries (five entries each of Benning-M, Benning-G, Benning-H, Benning-mgh, and Benning) were randomized within each block. The experimental unit for each entry was two 6.1-m rows spaced 76.2 cm apart. Each plot was end-trimmed to 3.6 m before harvest. For each plot data were recorded for maturity (date on which 95% of pods had reached their mature color), lodging (1, all plants upright to 5, all plants prostrate), and plant height (average distance from the soil surface to tip of three plants per plot). At maturity each plot was harvested with a self-propelled plot combine. To determine protein and oil content, a 50-g seed sample from each plot was sent to the USDA–ARS National Center for Agricultural Utilization Research at Peoria, IL., where an 18–20-g seed sample was evaluated with a model 1255 Infratec NIR Food and Feed Grain Analyzer (Ultra Tec Manufacturing, Inc., Santa Ana, CA). Protein and oil content are reported on a dry-weight basis. Seed quality scores were based on visual scores (1, very good to 5, very

poor). Seed weight (average weight of an individual seed) for each plot was evaluated from a 100-seed sample. Phenotypic data were analyzed by analysis of variance (ANOVA) with the Agrobase software (Generation II, Agronomix Software Inc., Winnipeg, MN, Canada). The statistical model assumed blocks and environments as random effects and NILs as fixed effects.

In 2005, seed yield of the same NILs was evaluated in two environments. A trial was planted on 23 May at the University of Georgia Plant Sciences Farm and the second was planted on 26 May at the University of Georgia Southwest Research and Education Center. Each trial was arranged in a randomized complete block design with four replications. In total, 12 entries (three entries each of Benning and Benning-MGH; two entries each of Benning-M, Benning-H, and Benning-G) were randomized within each block. The experimental unit for each entry was the same as the 2004 tests. Before harvest, plots were end-trimmed to 3.6 m. Agronomic data for each genotype was collected and analyzed as described for the 2004 experiments.

Antixenosis resistance in SIR NILs was assessed for corn earworm and soybean looper in a greenhouse using the same procedure described by All et al. (1989). Corn earworm and soybean looper eggs were supplied by the Crop Protection and Management Unit (USDA–ARS, Tifton, GA) and Benzon Research (Carlisle, PA), respectively. Three seeds of each entry were planted per 450-ml polystyrene foam cups, with three holes punched in its bottom to allow for drainage and water uptake. The cups were filled with Fafard 2 mix (Conrad Fafard, Agawam, MA). Each cup was thinned to one plant after 5 d. Cups were then organized in a randomized complete block experimental design with six replications. Five lines of each SIR QTL (Benning-mgh, Benning-M, Benning-G, and Benning-H), along with one entry each of Benning and PI 229358, were included in each block. Benning (susceptible) and PI 229358 (resistant) were also planted as a border in alternating fashion around all six blocks. The defoliation scores for each cup (average of three individuals) were analyzed by ANOVA with the Agrobase software (Generation II, Agronomix Software Inc., Winnipeg, MN, Canada).

The level of antibiosis to corn earworm and soybean looper for the SIR QTL in each NIL was evaluated in a growth chamber by a procedure used previously by Walker et al. (2002). The experiment included the 25 previously described NILs along with five entries each of Benning and PI 229358. The assays were arranged in a randomized complete block design with six blocks. The average weight of surviving larvae from three individual dishes (corn earworm) or in one dish (soybean looper) were recorded and analyzed by ANOVA with Agrobase software (Generation II, Agronomix Software Inc.).

For the marker analysis, DNA was extracted from unexpanded trifoliolate leaves of the 25 NILs greenhouse-grown plants by using a modified cetyltrimethylammonium bromide procedure as described by Zhu et al. (2006). For polymerase chain reaction (PCR) amplification (32 cycles, 94°C for 1 min, 94°C for 30 s, 46°C for 30 s, 68°C for 30 s, and held at 10°C after final cycle), reaction mixtures contained 20 ng of genomic DNA, 0.5 μM of forward and reverse primers (Perry Cregan, USDA–ARS Beltsville, MD), 2 mM of each dNTP, 2.5 mM Mg^{2+}, 1× PCR buffer (Promega, Madison, WI), and 0.5 U of *Taq* polymerase (Promega) in a total volume of 10 μl. The separation of PCR amplicons was conducted using 4.8% polyacrylamide gels run on an ABI PRISM 377 DNA Sequencer (Applied Biosystems, Foster City, CA). Samples were prepared for electrophoresis by combining 3 μl of PCR product, 2 μl of formamide, 0.75 μl of loading buffer, and 0.30 μl of GENESCAN-500 ROX DNA size standard (Applied Biosystems). Each was denatured for 5 min at 95°C, and 1.5 μl of each sample was loaded in the appropriate well of a 96-lane gel. Gels were scored visually based on marker size data from each parent to determine the SSR marker genotype of each line.

The previously described SSR marker methodology was used to evaluate the relative amount of PI 229358 genome present in the genomic regions of NILs harboring SIR-M, SIR-G, and SIR-H. Graphical genotypes were determined by SSR fingerprinting individual NILs in a 42–73-centimorgan (cM) region surrounding each introgressed SIR QTL. Distances between genetic markers were scaled to coincide with their actual estimated genetic distances (Song et al. 2004), and crossover points are represented midway between the two flanking markers (Fig. 1). It was presumed that no double crossovers in a single meiosis had occurred between markers.

Results and Discussion

Based on the average percentage of defoliation and larval weights, Benning was the most susceptible and PI 229358 the most resistant to corn earworm and soybean looper, as expected (Table 1). Significant differences for each insect and each genotype were determined using a restricted least-significant difference (*F*-least significant difference [LSD]) after the detection of a significant *F*-statistic in the ANOVA. For corn earworm, the level of defoliation ($F = 2.16$; df = 29, 144; $P < 0.05$) and larval weight ($F = 4.98$; df = 29, 142; $P < 0.05$) for Benning-M lines were found to be similar to those of PI 229358. Although Benning-M and PI 229358 were equally defoliated by soybean looper, the larvae that fed on Benning-M were on average 10.9 mg heavier than those that fed on PI 229358. The Benning-M lines lack SIR-G, whereas PI 229358 does not, which may account for the difference in larval weight between the two.

The effect of SIR-M was detected in corn earworm and soybean looper antixenosis screens ($F = 2.03$; df = 29, 145; $P < 0.05$), as Benning-M lines were significantly less defoliated than Benning (7% less for corn earworm and 13% less for soybean looper) and the Benning-mgh control (5% less for corn earworm and 15% less for soybean looper). Similarly, larval weights were 25 mg less for corn earworm and 26 mg less for

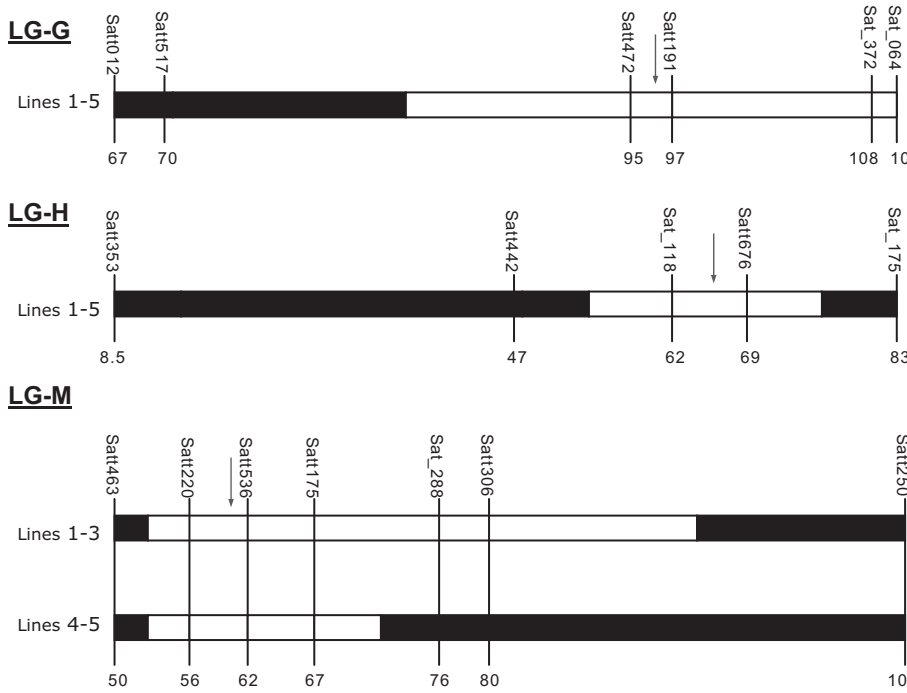

Fig. 1. Graphical genotypes of NILs representing amount of PI 229358 genome flanking SIR-G, SIR-H, and SIR-M. Numbers shown under each SSR locus represent the approximate centimorgan location of the marker on the USDA–ARS consensus linkage group (Song et al. 2004). The most likely position of the SIR QTL is indicated by an arrow. White segments indicate PI 229358 origin, and black segments indicate Benning origin. It was assumed that genomic regions defined by a single marker extended halfway to its flanking marker(s).

soybean looper when the insect was provided SIR-M leaves rather than Benning leaves. When Benning-M lines were compared with the Benning-mgh control, Benning-M significantly reduced corn earworm larval weights by 16 mg, but not soybean looper larval weights ($F = 2.30$; df = 29, 103; $P < 0.05$). One replication of the soybean looper antibiosis tests was dropped due increased levels of larval mortality after day 1 of the bioassay. No significant ($P = 0.05$) effects were detected for SIR-G and SIR-H compared with Benning-mgh for corn earworm and soybean looper antibiosis or antixenosis.

When Benning-H and Benning-G NILs were compared with the Benning recurrent parent, the weight of soybean looper larvae were reduced by ≈17 mg for both SIR QTLs. Other than this finding, these results support those reported by Zhu et al. (2006), who compared defoliation and larval weight in lines containing combinations of SIR QTLs and determined that SIR-G and SIR-H must be in combination with PI 229358 alleles at SIR-M to provide significant reductions in defoliation and larval weights.

The recurrent parent, Benning, averaged 335 kg ha^{-1} higher yield than Benning-G (Table 2). Lines containing SIR-G averaged the lowest mean seed weight (126 mg $seed^{-1}$) of all NILs, which was 9 mg $seed^{-1}$ less than Benning. The Benning-M NILs had significantly larger seed than all other entries.

Table 1. Mean percentage of defoliation of SIR QTL NILs by corn earworm and soybean looper and larval weight from feeding assays (lower numbers indicate greater resistance)

	Corn earworm		Soybean looper	
	Defoliation (%)	Larval wt (mg)	Defoliation (%)	Larval wt (mg)
	(mean ± SD)[a]	(mean ± SD)[a]	(mean ± SD)[a]	(mean ± SD)[b]
PI229358	24.6 ± 3.5a	22.1 ± 6.8a	32.0 ± 3.0a	18.0 ± 12.7a
Benning-M	28.2 ± 4.1ab	20.8 ± 3.0a	33.7 ± 4.6a	28.9 ± 12.9b
Benning-H	32.7 ± 1.8c	42.7 ± 8.4b	47.0 ± 4.9b	38.2 ± 27.0b
Benning-G	31.5 ± 1.7bc	40.5 ± 6.9b	45.7 ± 6.4b	38.1 ± 13.5b
Benning-mgh	33.4 ± 2.5c	37.2 ± 10.2b	48.3 ± 2.8b	34.9 ± 7.6bc
Benning	35.3 ± 2.8c	45.5 ± 11.4b	46.8 ± 3.9b	55.0 ± 19.5d

Means within a column followed by the same letter are not significantly different ($P > 0.05$; Fisher's restricted LSD test).
[a] Average of six replicates, five lines per replicate.
[b] Average of five replicates, five lines per replicate.

Table 2. Mean agronomic performance (±SD) of five lines of each SIR QTL NIL genotype by using three replications at three locations in 2004

Near-isogenic line	Seed yield (kg/ha^{-1})	Plant ht (cm)	Lodging (score)	Oil (g/kg^{-1})	Protein (g/kg^{-1})	Seed quality (score)	Wt (mg/seed^{-1})
Benning	2840 ± 94a	99 ± 2.5a	4.0 ± 0.13a	196 ± 2.0a	382 ± 2.8a	1.72 ± 0.06a	135 ± 2.8b
Ben-mgh	2756 ± 72a	98 ± 3.9a	4.0 ± 0.28a	194 ± 1.0a	385 ± 2.7a	1.68 ± 0.11a	127 ± 2.7c
Ben-M	2779 ± 108a	100 ± 2.2a	4.4 ± 0.19a	193 ± 1.7a	388 ± 2.1a	1.69 ± 0.08a	146 ± 2.1a
Ben-H	2755 ± 83a	93 ± 1.6b	4.2 ± 0.20a	192 ± 1.3a	387 ± 1.0a	1.69 ± 0.11a	139 ± 1.0b
Ben-G	2505 ± 51b	99 ± 2.4a	3.9 ± 0.31a	195 ± 1.9a	386 ± 3.0a	1.68 ± 0.07a	126 ± 2.3c

Means within a column followed by the same letter are not significantly different ($P > 0.05$; Fisher's restricted LSD test).

For other agronomic traits, significant differences were detected among the SIR QTL NILs for plant height (centimeters), whereas no significant differences were detected for seed oil, seed protein, or seed quality (Table 2). Benning-H lines were on average 6 cm shorter than Benning, and 5–7 cm shorter than the other SIR QTL NILs.

The SIR NILs were also evaluated in 2005 in two environments along with Benning-MGH and Benning lines. Benning-mgh lines were not included in the test due to an oversight, but 'Benning' served as a suitable check because it is genetically identical to Benning-mgh. In 2005, Benning-H and Benning were significantly higher in seed yield than all other entries (Table 3). The lowest yielding entries were Ben-MGH and Benning-G. These NILs averaged 340 kg ha^{-1} lower yield than Benning. Over the five combined environments, the Benning-G NILs averaged ≈283 kg ha^{-1} less seed yield than Benning, whereas Benning-M and Benning-H were similar in yield to Benning (Table 4).

In 2005, significant differences for plant height, lodging, seed quality, and seed weight were found among the SIR NILs (Table 3). No significant differences were detected for seed oil or seed protein. Similar to 2004, the Benning-H lines were significantly shorter than all other lines evaluated, whereas the Benning-G lines again showed the smallest seed weight.

Graphical genotypes were constructed for SIR-M, SIR-G, and SIR-H NILs as a means of assessing the relative amounts of PI 229358 genome remaining in each NIL near the introgressed SIR QTL (Fig. 1). SSR marker loci residing within the genomic regions not included in the graphical genotypes were monomorphic between Benning and PI 229358.

Graphical genotypes surrounding SIR-G cover a 42-cM region based on six polymorphic SSR markers, with ≈26 cM of PI genome surrounding the QTL for the SIR-G NIL. A seventy-three cM region containing five polymorphic SSR markers was evaluated for the Benning-H graphical genotypes, with 23 cM of PI 229358 genome remaining in all five of the SIR-H NILs. Benning-M graphical genotypes represented a 58-cM region based on seven polymorphic SSR markers surrounding SIR-M. Three of the five Benning-M NILs (L1, L2, and L3) contain ≈41 cM of PI 229358 genome, spanning from Satt220 to Satt306. NIL L4 and L5 have PI 229358 alleles between Satt220 and Satt175, roughly an 11-cM distance, indicative of an additional crossover event in this region upstream of SIR-M (Fig. 1). No significant differences in agronomic performance were detected among the individual SIR-M lines. SIR-M was recently fine-mapped using recombinant substitution lines derived from a Benning (7) × PI 229358 population to a 0.52 cM interval between Sat 258 and Satt702 (Zhu et al. 2006). It is unknown whether a single gene or a cluster of related genes residing within this interval conditions the higher level of resistance associated with the SIR-M locus. This increased resolution at SIR-M provides improved marker precision and should facilitate ongoing efforts to clone SIR-M.

No significant differences in resistance to corn earworm or soybean looper could be detected among the five Benning NILs, again reaffirming that SIR-M is likely located in the region between Satt220 and Satt536 on LG M (Zhu et al. 2006). As expected, the Benning-mgh lines possess Benning alleles at all marker loci used to genotype Benning-M, Benning-G, and Benning-H NILs in the region containing the appropriate SIR QTL (data not shown).

Our results indicate there was not a yield reduction associated with SIRQTL-M or SIRQTL-H NILs. Thus, these SIR QTLs could be introgressed from these NILs

Table 3. Mean agronomic performance of five SIR QTL NILs (three entries for Benning and two lines each of Benning-MGH, Benning-M, Benning-H, and Benning-G) at two 2005 locations

Near-isogenic line	Seed yield (kg/ha^{-1})	Plant ht (cm)	Lodging (score)	Oil (g/kg^{-1})	Protein (g/kg^{-1})	Seed quality (score)	Wt (mg/seed^{-1})
Benning	3426 ± 148a	93 ± 7.5b	1.5 ± 0.15bc	205 ± 0.6a	410 ± 1.5a	2.5 ± 0.06ab	143 ± 3.2bc
Ben-M	3244 ± 23b	99 ± 2.1ab	2.1 ± 0.07a	201 ± 2.8a	414 ± 0.7a	2.4 ± 0.07bc	151 ± 3.5a
Ben-H	3500 ± 33a	91 ± 2.1b	1.6 ± 0.02bc	202 ± 0.7a	409 ± 2.8a	2.2 ± 0.21c	147 ± 4.2ab
Ben-G	3095 ± 99bc	103 ± 4.9a	1.4 ± 0.07c	202 ± 3.5a	414 ± 0.4a	2.5 ± 0.02ab	128 ± 1.4d
Ben-MGH	3073 ± 22c	95 ± 4.0ab	1.7 ± 0.15b	204 ± 3.7a	409 ± 1.6a	2.7 ± 0.06a	138 ± 2.3c

Means within a column followed by the same letter are not significantly different ($P > 0.05$; Fisher's restricted LSD test).

Table 4. Mean yield (kg/ha^{-1}) of five SIR NILs and Benning in 2004 and 2005

Near-isogenic line	2004 (3 locations)	2005 (2 locations)	2004/2005 (5 locations)
Benning	2,840a	3,426a	3,133a
Benning-mgh	2,756a	—	
Ben-M	2,779a	3,244b	3,067a
Ben-H	2,755a	3,500a	2,949a
Ben-G	2,505b	3,096bc	2,741b
Ben-MGH	—	3,073c	

Means within a column followed by the same letter are not significantly different ($P > 0.05$; Fisher's restricted LSD test).

into other cultivar backgrounds without an expected yield drag.

A significant seed yield reduction was associated with our SIR-G NILs. It is also apparent that seed weight is reduced in these NILs. Mian et al. (1996) and Lee et al. (2001) each detected a QTL at the RFLP locus A235 on LG G, associated with seed weight in the two mapping populations PI97100 × 'Coker 237' and 'Pureunkong' × 'Jinpumkong', respectively. This RFLP locus maps within 2 cM of the SSR markers, Satt191 and Satt472, which flank SIR-G. One possible scenario is that SIR-G imposes a metabolic cost that decreases yield. However, it is more probable that SIR-G is linked to another QTL for seed weight.

The ≈26-cM segment of PI 229358 genome surrounding this QTL is at the distal portion of LG-G, where the availability of informative SSR markers are limited. To make substantial progress in our efforts to eliminate the yield drag associated with SIRQTL-G, it will be necessary to create and identify lines containing crossovers within this specific region of LG G. This task would be made easier by the development of additional PCR-based markers.

The Georgia Agricultural Experiment Stations has recently approved the release of SIR germplasm (Benning NILs with introgressed SIR-M, SIR-G, SIR-H, and SIR-MGH from PI 229358) with the aim of providing this material to soybean breeders and entomologists for further study and for use in development of SIR cultivars (Zhu et al. 2007).

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