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RESEARCH

Joint Linkage QTL Mapping for Yield and Agronomic Traits in a Composite Map of Three Common Bean RIL Populations

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ABSTRACT

Bean (*Phaseolus vulgaris* L.) production is challenged by many limitations with drought being among the top causes of crop failure worldwide. In this study, we constructed three small-red-seeded bean recombinant inbred line (RIL) mapping populations (S48M, S94M, and S95M) with a common parent ('Merlot') and performed joint interval mapping analysis as a small nested association mapping (NAM) population for agronomic traits and performance under rainfed conditions in Michigan. The objective was to identify novel sources of improved performance and genomic regions associated with desirable traits under rainfed and water-sufficient conditions in small-red bean breeding materials adapted to temperate zones. A composite linkage map was constructed using single-nucleotide polymorphism (SNP) markers from the three populations and resulted in an improved version of the individual linkage maps shown by a greater genome span covered in the composite map (909 cM). A number of quantitative trait loci (QTL) of different size effects were identified for seed yield (R^2 = 15.4–30.7%), seed size (R^2 = 16.4–20.2%), days to flowering (R^2 = 12.4–36.1%), days to maturity (R^2 = 16.2%), lodging score (R^2 = 10.3–12.9%), and canopy height (R^2 = 17%). Our study confirmed previously reported QTL on five chromosomes and identified a new QTL for canopy height on chromosome Pv10. The use of a composite map and QTL analysis under a NAM population structure increased our ability to detect small-effect QTL that were segregating in at least two of the populations but would not have been detected using individual linkage maps.

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Abbreviations: DII, drought intensity index; DSI, drought susceptibility index; G × Y, genotype × year; GO, gene ontology; GWAS, genome-wide association study; H^2, broad-sense heritability; JICIM, joint inclusive composite interval mapping; NAM, nested association mapping; QTL, quantitative trait loci; RIL, recombinant inbred line; SNP, single-nucleotide polymorphism; SVREC, Saginaw Valley Research and Extension Center.

Dry or common bean production is limited by many factors with drought being the most important worldwide (Assefa et al., 2015). An estimated 60% of common bean production is affected by drought (Beebe, 2012; White and Singh, 1991). In the eastern United States, common bean is produced predominantly under rainfed conditions as opposed to the semiarid western United States, where irrigation is necessary to produce a successful bean crop (Munoz-Perea et al., 2006). Drought is undoubtedly a major target for bean improvement programs particularly in the recent decades with the increased importance of the future impact of climate change on agriculture (Beebe et al., 2011). The improvement of quantitatively inherited agronomic traits involved in drought tolerance under variable rainfed production systems has been difficult, resulting in slow progress toward ameliorating the constraint in common bean (Cattivelli et al., 2008).

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To improve cultivar performance under water-limiting conditions, it is necessary to identify genetic variation for traits associated with stress-tolerance mechanisms that are relevant to a particular environment. Previous genetic studies in common bean have determined that local adaptation to drought is necessary to develop superior cultivars that serve as parents of improved populations (White et al., 1994a,b). The Durango race of common bean (Singh et al., 1991) is commonly used as a source of drought tolerance in the common bean improvement programs, and the combination of the Durango and Mesoamerica races has also been a reliable source of germplasm with improved performance under drought stress (Frahm et al., 2004; Ishitani et al., 2004). In an intergene pool cross, Mukeshimana et al. (2014a) found a number of yield and yield-component QTL in a recombinant inbred line (RIL) population (SEA5/CAL96) grown under drought conditions in Rwanda. The SEA5 parent was a cream-colored, drought-tolerant bean line from double cross between parents from races Mesoamerica and Durango, whereas CAL96 is a red-mottled, large-seed Andean bean that is widely grown in East Africa that lacks drought tolerance. Major QTL for yield and agronomic traits have also been detected under multiple terminal drought-stress environments in the western United States in a RIL population generated from the cross of two Durango race cultivars, 'Buster' and 'Roza' (Trapp et al., 2015).

Modest progress has been made in developing drought-stress tolerance in a number of different bean market classes (Asfaw and Blair 2012; Beebe et al., 2008; Frahm et al., 2004; Miklas et al., 2006; Mukeshimana et al., 2014a; Schneider et al., 1997), whereas the small-red market class grown in the United States has not undergone significant changes toward improving performance under drought stress (Assefa et al., 2015). Prior attempts to improve drought tolerance in the small-red market class for Central America were made by Beebe et al. (2008), and several studies have found QTL associated with desirable traits under drought conditions using the DOR364/BAT477 RIL population (Blair et al., 2012). BAT477 is a small cream-colored bean from the Mesoamerica race with a type-II growth habit that was used as the drought-tolerant parent because of its rooting and water use characteristics (Sponchiado et al., 1989; White and Castillo, 1989). However, BAT477 is lacking in agronomic performance and commercial seed traits, whereas DOR364 is a Mesoamerican type-II bean with good agronomic performance, preferred small-red seed type, and disease resistance (Beebe et al., 1995). Other studies report QTL for traits such as yield, canopy biomass, pod harvest index, total nonstructural carbohydrates, SPAD chlorophyll, leaf area index, and canopy temperature depression (Asfaw et al., 2012), while others have focused on root traits such as rooting depth, rooting length, and root biomass (Asfaw and Blair, 2012). The QTL for root traits that could be functional in drought tolerance were detected in a RIL population developed between breeding lines DOR 364 and G19833 (Beebe et al., 2006). Prior QTL studies on drought in common bean have focused on RIL populations that analyze single biparental crosses, which limit the power of QTL detection.

In common bean, efforts have been made previously to integrate genetic linkage maps. The first reports of map integration in common bean were published from a project to develop genomic libraries (Nodari et al., 1992), construct an anchoring linkage map (Nodari et al., 1993), and using the map to group markers between previously existing populations, other linkage maps, and marker data to create denser, more robust integrated map (Freyre et al., 1998). This integrated map established the foundation for other groups to integrate additional information from new mapping populations and new marker types (Blair et al., 2003). Other reports have integrated maps via the use of pooled restriction fragment length polymorphism clones (Pedrosa et al., 2003) and validated them via fluorescence in situ hybridization. More recently, Galeano et al. (2011) developed a saturated map of DOR364/BAT477 and compared it with the previously reported linkage maps of BAT93/Jalo EEP558 and DOR364/G18933 to build a saturated consensus map with SNP markers.

An alternative to developing saturated maps is to integrate the advantages of linkage and association mapping with the increased resolution of dense marker arrays in a NAM design (McMullen et al., 2009). Whole-genome scans using NAM designs have proven more powerful in the detection of QTL with different size effects (Yu et al., 2008). In this study, we constructed three small-red-seeded RIL mapping populations with a common parent and performed joint interval mapping analysis as a NAM population for agronomic traits and performance under rainfed conditions. The objective was to identify novel sources of improved performance and genomic regions associated with desirable traits under rainfed and water-sufficient conditions in small-red bean breeding materials adapted to temperate zones.

MATERIALS AND METHODS

Plant Material

Three half-sib mapping populations were generated using the cultivar Merlot as a common parent crossed to the breeding lines SER48, SER94, and SER95. The three SER lines were developed at the International Center for Tropical Agriculture (CIAT) in Cali, Colombia, and were developed in an effort to introduce tolerance to terminal drought into the small-red, black, cream, and carioca market classes. The small-red SER lines were developed from double and triple crosses between multiple parents, some of which originated from the Durango race such as SEA15. Other parents had no Durango race parentage but were identified as drought tolerant in field evaluations.

The full description on the development of the SER lines for tropical regions is described by Beebe et al. (2008). The common parent, Merlot, in the three RIL populations belongs to the US small-red market class and is a widely grown cultivar in this class. The traditional US small-red market class is largely comprised of race Jalisco germplasm, whereas small-red SER lines are largely Mesoamerica with introgression from race Durango. Merlot, released in 2004, was derived from cross of breeding lines ARS-R94037 and ARS-R94161 that had parentage from the Jalisco, Mesoamerica, and Durango races of common bean (Hosfield et al., 2004). The cultivar possesses an upright indeterminate type IIA growth habit, multiple disease resistance, and excellent canning quality (Hosfield et al., 2004). In contrast, Merlot was selected at a time when drought-tolerance traits were not a significant part of the selection process; therefore, Merlot has superior performance during normal rainfall years but has exhibited significant reduced performance during recent drought years. The intention for these crosses was to introduce improved performance under drought into the US small-red market class by crossing Merlot to efficient small-red, drought-tolerant SER lines with high harvest indexes. For the development of the RILs, crosses were made in the greenhouse, seed was advanced to the F_2 generation in the field, where a single pod was collected from each plant, and advanced as single seed descent until the $F_{4:5}$ generation for replicated trials. The RIL populations developed were SER48/Merlot (76 lines), SER94/Merlot (48 lines), and SER95/Merlot (36 lines) and will be henceforth designated as populations S48M, S94M, and S95M, respectively. Several other populations were generated with Merlot as the common parent, but only those with the greatest number of lines were used in this study.

Phenotyping

The populations were evaluated at the Saginaw Valley Research and Extension Center (SVREC) in Richville, MI, in 2013 and 2014. The SVREC is located at 43°4′ N, −83°7′ W. The soils at this site are a Tappan–Londo loam complex (fine-loamy, mixed, active, calcareous, mesic Typic Enduaquolls and fine-loamy, mixed, semiactive, mesic Aeric Glossaqualfs). Each population was planted as an appropriately sized α-lattice design determined by population size with three replications. The plots were planted as two center rows of the line with a row of border on each side; each plot was 4.5 m in length with 0.5 m between rows. All of the parents were planted in every trial as checks. The populations were evaluated for their agronomic performance as well as yield, seed size, and a response to water deficit. The agronomic traits included days to flowering, canopy height, lodging, and days to maturity. The days-to-flowering trait was measured as the number of days from planting to the day where 50% of the plants in the plot showed flowers. Maturity was determined as the number of days after planting when the plot was completely senesced and ready to harvest. Canopy height was determined as the distance from the soil to the last expanded leaf as an average across the plot. Yield was determined by harvesting 4 m of the two middle rows, open-air drying the harvested seed, and correcting the samples to 18% moisture. Seed size was determined as the weight of 100 seeds corrected at 18% moisture. A wilting score was measured on the plants every time contrasting wilting symptoms were observable across the field; wilting score involves a rating from 0 to 100, where 0 is no visible stress causing wilting and 100 is complete death from water stress. Lodging score was measured from 1 to 5 with 1 as fully upright and 5 as fully lodged or if stem base breakage occurred. Further details on wilting scores can be found in King et al. (2009).

Genotyping

Genomic DNA was extracted from each of the lines using an Omega Bio-Tek Mag-Bind Plant DNA Plus kit (Omega Bio-Tek Inc.) with the December 2013 version protocol, product number M1128-01. Tissue was collected from young leaves and frozen at −80°C for 3 d in 96-well plates and the tissue was disrupted by placing tungsten carbide beads in each well and the plates onto a plate shaker (MO BIO). After tissue grinding, the protocol was followed per protocol instructions. Buffer plates were prepared separately and introduced into an extraction protocol along with the Mag-Bind into a KingFisher Flex magnetic particle processor (Thermo Scientific). Once extractions were complete, DNA was quantified using a Picogreen fluorescent dye-based assay, measured in a fluorometer, and determined by regression against a standard sample of known DNA concentration. The final DNA plates were submitted to the USDA genotyping facility in Beltsville, MD, to be analyzed using the BARCBean6k_3 BeadChip phenotyping platform. This resulted in a total of 5398 SNPs called via the genotyping module of the GenomeStudio (Illumina Inc.) software. Details on the construction of the SNP array are provided in Song et al. (2015) and Schmutz et al. (2014).

Statistical Analyses

Field evaluation data was analyzed using linear mixed models using the PROC MIXED statement in SAS v9.0 (SAS Institute, 2011). Each population was analyzed separately as a lattice design with three replications. Random effects included incomplete blocks (iblock) nested within years and replications (rep) and replications were nested within years; lines (G), years (Y), and their interaction (G × Y) were fixed effects. Trial years were considered as environments to determine genotype × environment interaction. The best model was chosen based on the Akaike information criterion, resulting in the following model:

$$Y_{ijkl} = \mu + \text{iblock}_i\left(\text{year}_j\text{rep}_k\right) + \text{rep}_k\left(\text{year}_j\right) + \text{line}_l + \text{year}_j + (\text{genotype}_l \times \text{year}_j) + e_{ijkl}$$

Broad-sense heritability (H^2) was estimated for traits on an entry-mean basis using the variance component method (Fehr, 1987; Hallauer et al., 2010) defined as follows:

$$H^2 = \frac{\sigma^2_g}{\frac{\sigma^2_e}{r\gamma} + \frac{\sigma^2_{gy}}{\gamma} + \sigma^2_g}$$

Where σ^2_g is the total genetic variance, σ^2_e is the experimental error, σ^2_{gy} is the G × Y interaction, r is the replications, and γ is the years.

As a measure of the intensity of drought across years and within parents and RILs, drought intensity index (DII) and drought susceptibility index (DSI) were calculated (Schneider et al., 1997). The DII was calculated as $\mathrm{DII} = 1 - \left(\frac{\mathrm{Xd}}{\mathrm{Xp}}\right)$, where Xd is the overall drought stress mean and Xp is the overall nonstress mean. The DSI was calculated as $\mathrm{DSI} = \frac{\left[1 - \left(\frac{\mathrm{Yd}}{\mathrm{Yp}}\right)\right]}{\mathrm{DII}}$, where Yd and Yp are the drought stressed and nonstressed genotypic means, respectively (Fischer and Maurer, 1978). Pearson correlations among traits were also estimated.

Map Construction and Quantitative Trait Loci Mapping

Marker filtering was done on the basis of genotyping errors, missing data, and polymorphism. Markers with more than 50% missing data were eliminated. Genotyping errors were corrected by genotyping the parents of each mapping population in duplicate and only keeping the markers with consistent calls across replications. Marker polymorphism was determined for every parent pair, and monomorphic markers were deleted for each population even if this included deleting some polymorphic markers in other populations. This ensured that only polymorphic markers were kept across the three populations for composite map construction. Heterozygous and missing markers in any parent were also removed.

Before construction of linkage groups, identical markers were eliminated and markers with segregation distortion declared as significant by the Chi-squared test were also eliminated. The software Joinmap 4.0 (Van Ooijen, 2006) was used for map construction. Separate datasets for every chromosome were generated based on prior knowledge of their physical positions in common bean genome (Schmutz et al., 2014). Linkage groups were estimated using the linkage logarithm of odds (LOD) grouping parameter in Joinmap, and groups with a LOD value larger by at least 10 were selected.

A composite linkage map was built by pooling the filtered marker data of the three populations. Map construction proceeded by using both the regression mapping and maximum likelihood algorithms to evaluate agreement among the produced maps. Regression mapping was set to use linkages with a recombination frequency <0.3 and a LOD >3; the Kosambi (Kosambi, 1943) mapping function was used. For the maximum likelihood algorithm, map order optimization parameters were set to a chain length of 10,000 iterations (also for multipoint estimation of recombination frequencies), 2000 iterations burn-in, and four cycles. Additionally, a map with the fixed-orders option in Joinmap was generated with the physical order of the markers. Upon completion of the three map construction methods, marker ordering and map orientation were verified by inspecting the alignment between the two methods and the map ordered with physical positions; once a finalized map version was determined for a given chromosome, the map constructed using the maximum likelihood method was retained.

Quantitative trait loci detection was performed using the QTL ICIMapping software (Wang et al., 2012); phenotypic and genotypic data for the three populations were treated as a NAM population using the NAM module of the software. Joint inclusive composite interval mapping (JICIM), reported in Buckler et al. (2009) and Li et al. (2011), was used to detect QTL at a significance threshold set from the average of the top 5% of 1000 permutations considering type-I error rate of 0.05. The mapping parameter for step-between marker intervals was set at 1 cM. Once QTL intervals were obtained, SNP relative positions were converted into physical positions, and the genes in that interval were retrieved from the *P. vulgaris* v1.0 gene annotation file located in the Phytozome database (Goodstein et al., 2012). This search resulted in a list of the genes located in that interval, gene ontology (GO) terms, best match to the *Arabidopsis thaliana* genome, and a description of this match. Gene ontology enrichment analysis was also performed to determine groups of genes with significant probabilities that a given number of the given set of genes belong to a particular GO term. This analysis results in gene groups with significant ontology terms for biological processes, cellular components, or molecular functions. The tables with the genes located in the intervals and the GO enrichment analysis results of QTL with significant results are found in the Supplemental Materials (Supplemental Table S1–S19).

RESULTS AND DISCUSSION

Environment

Mean air temperature, topsoil moisture, and daily precipitation during the 2013 and 2014 seasons at SVREC are reported in Fig. 1. During the 2013 and 2014 growing seasons (June–September) a total of 155 and 345 mm of rainfall were recorded, respectively. The 2013 growing season precipitation was well below the averages of 292 and 335 mm between the 1951–1980 and 1971–2000 30-yr periods, respectively, according to the Michigan State University Office of Climatology Records (http://climate.geo.msu.edu/climate_mi/stations/7227/). In contrast, the 2014 growing season presented higher total precipitation than the long-term means. Better precipitation distribution was observed when compared with the 2013 season, particularly during the flowering and initial pod filling stages in July 2014. During for the 33 to 50 d after planting period, the 2013 and 2014 growing seasons had 14 and 79 mm, respectively. Mean daily temperatures for the month of July (24–56 d after planting) in 2013 and 2014 were 21.3 and 19°C, respectively. Based on the precipitation and temperature data, it is possible to separate the 2 yr as water deficient (2013) and water sufficient (2014).

Phenotypic Data

Means of the traits measured are presented in Table 1 along with the significance for the genotype, year, and G × Y effects from the analysis of variance. A distinction in drought-stress level was observed between the 2 yr based on DII for yield. The DII was 0.47, 0.55, and 0.42 for S48M, S94M, and S95M, respectively. Seed size was only

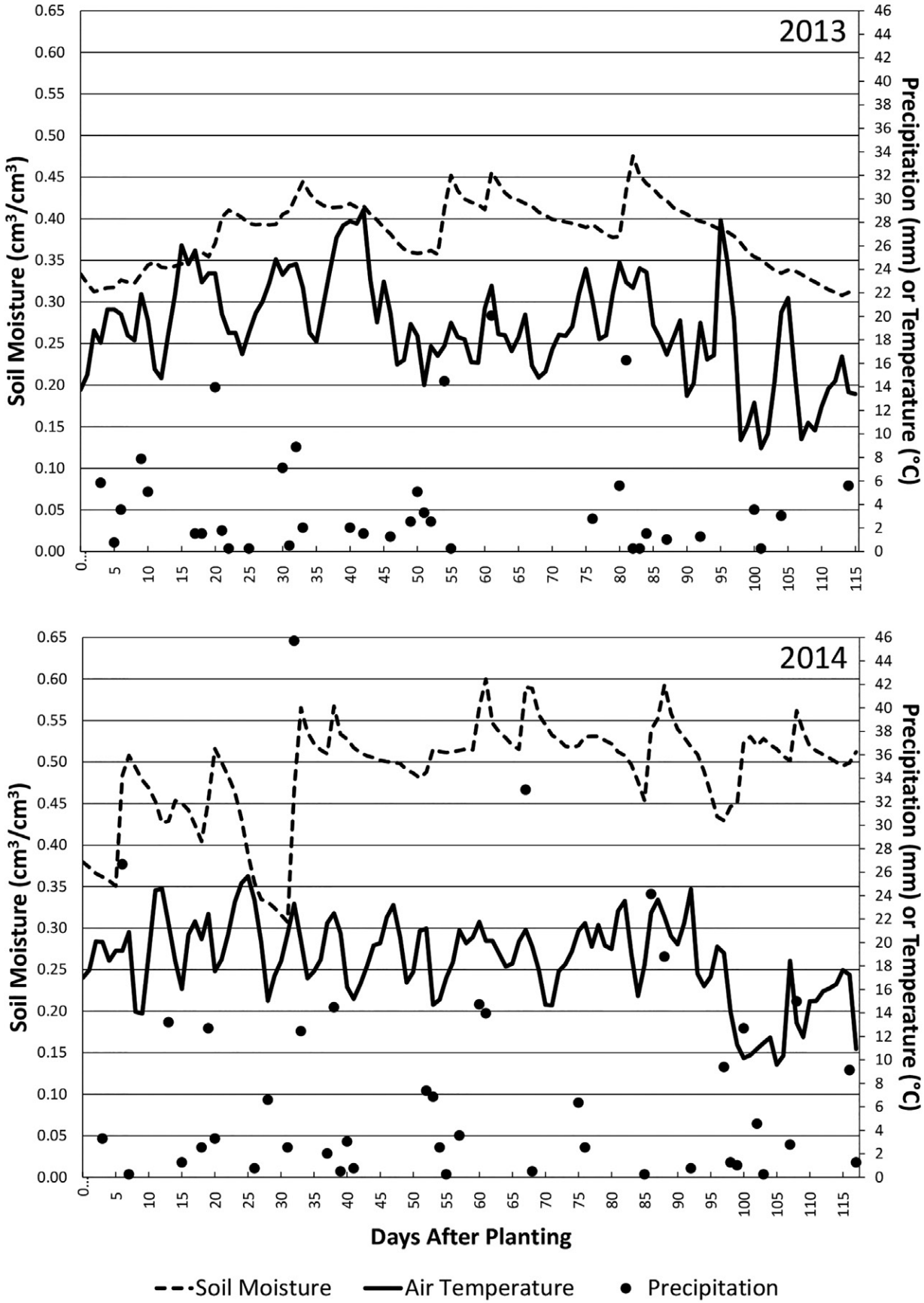

Fig. 1. Mean soil moisture, precipitation, and mean air temperature for the 2013 (top) and 2014 (bottom) growing seasons at the Saginaw Valley Research and Extension Center, Richville, MI. Soil moisture values are plotted on the left *y*-axis and precipitation and temperature on the right *y*-axis.

Table 1. Means, ranges, and effects among lines (G), years (Y), and lines × years (G × Y) for yield, seed weight, days to flower and maturity, canopy height, lodging, and wilting score for the S48M, S95M, and S94M populations grown in 2013 and 2014 at the Saginaw Valley Research and Extension Center, Richville, MI.

Population and trait†	2013			2014			Mean§				ANOVA		
	SER	Merlot	RIL (Range)‡	SER	Merlot	RIL (Range)§	SER	Merlot	RIL	H^2 (95% CI)¶	G	Y	G × Y
S48M													
SY (kg ha^{-1})	1403	2167	1828 (3171–868)	3114	3549	3468 (5796–1954)	2091	2774	2511	0.67 (0.52–0.77)	***	***	***
SW (g 100 seed^{-1})	31.9	33.4	30.7 (39.7–23)	35.6	39.2	36.8 (46.4–28)	33.8	36.3	33.8	0.81 (0.72–0.87)	***	***	**
DF	39.0	41.5	40.7 (47–37)	39.0	43.0	41.8 (49–38)	39	42.3	41.3	0.93 (0.89–0.95)	***	NS	NS
HT (cm)	40.0	55.0	50.3 (75–30)	27.5	48.3	37.1 (55–15)	33.8	51	43.7	0.64 (0.47–0.75)	***	*	**
LDG (1–7)	1.5	2.0	2.5 (5–1)	5.5	3.3	3.9 (7–1)	3.5	2.8	3.2	0.71 (0.57–0.8)	***	*	***
DM	95	102	99.8 (110–85)	102	102	102.1 (105–102)	99	102	101	0.05 (−0.49–0.3)	NS	NS	NS
WS (0–100)	35.0	27.5	36.6 (65–20)	N/A	N/A	N/A	N/A	N/A	N/A	0.10 (−0.31–0.37)	N/A	N/A	N/A
S94M													
SY (kg ha^{-1})	1119	2701	1823 (3421–532)	3021	4112	3984 (5768–1958)	1839	3333	2695	0.80 (0.67–0.87)	***	***	***
SW (g 100 seed^{-1})	23.5	34.0	28.6 (36.3–22.9)	29.9	40.4	34.7 (45.1–28.1)	26.7	37.2	31.7	0.85 (0.75–0.91)	***	***	***
DF	38.0	41.5	41.9 (48–37)	39.5	45.5	42.8 (50–30)	38.8	43.5	42.4	0.86 (0.78–0.92)	***	*	**
HT (cm)	30.0	50.0	45 (65–30)	25.0	42.5	37.4 (55–25)	27.5	46.3	41.1	0.70 (0.51–0.82)	***	*	*
LDG (1–7)	3.0	3.0	2.8 (5–1)	1.0	2.0	2.8 (7–1)	2	2.5	2.8	0.63 (0.4–0.77)	***	NS	**
DM	100	102.5	102.1 (110–90)	102	102	103 (112–102)	101.2	102.2	102.7	0.59 (0.34–0.75)	***	NS	***
WS (0–100)	35.0	36.5	33.2 (65–10)	N/A	N/A	N/A	N/A	N/A	N/A	0.08 (−0.69–0.31)	N/A	N/A	N/A
S95M													
SY (kg ha^{-1})	1275	2607	1860 (3076–725)	2690	4533	3217 (5163–1282)	1853	3438	2431	0.82 (0.68–0.9)	***	***	***
SW (g 100 seed^{-1})	25.7	34.0	29.5 (39.7–20.3)	31.8	40.1	33.8 (44.8–25.3)	28.7	37.1	31.7	0.84 (0.72–0.91)	***	**	*
DF	38.5	42.0	40.5 (48–37)	39.0	41.5	41.9 (49–37)	38.8	41.8	41.2	0.91 (0.84–0.95)	***	NS	NS
HT (cm)	37.5	70.0	45.4 (70–20)	37.5	47.5	39.4 (55–25)	37.5	58.8	42.4	0.85 (0.73–0.91)	***	NS	***
LDG (1–7)	2.5	1.5	2.5 (5–1)	1.0	2.0	2.1 (7–1)	1.8	1.8	2.3	0.68 (0.44–0.82)	***	NS	**
DM	102	103.5	102.4 (120–90)	102	102.7	102.7 (117–102)	102	103	102.6	0.62 (0.33–0.78)	***	NS	**
WS (0–100)	25.0	25.0	31.2 (50–10)	N/A	N/A	N/A	N/A	N/A	N/A	0.20 (−0.36–0.53)	N/A	N/A	N/A

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

† SY, seed yield; SW, seed size; DF, days to flowering; HT, canopy height; LDG, lodging score; DM, days to maturity; WS, wilting score.

‡ Range in values for individuals within recombinant inbred line (RIL) population.

§ Seed yield reported as geometric mean; all other traits reported as arithmetic means.

¶ H^2, broad-sense heritability.

moderately affected by drought with lower DII values of 0.12 to 0.18 across populations. Genotype × year interactions were significant for yield, seed size, and lodging score in all populations. Days to flowering only showed a significant G × Y interaction in the S94M population, which likely was due to the difference in drought stress between the 2 yr. Interestingly, days to flowering in the S48M population did not have a significant effect between years or G × Y, indicating that in this population, days to flowering was independent of the environment. Genotypic differences were significant for most of the traits in all populations with the exception of days to maturity in population S95M. Wilting scores were only measured in 2013, as it was the only year where wilting symptoms were clearly observable from increased drought stress, but no genotypic differences were found for wilting score in any of the populations.

The percentage variation for all of the traits was mostly attributed to genotypic effect, rather than G × Y interactions. In the case of seed yield, lines accounted for 20.7, 19.4, and 44.7% of the variation, whereas G × Y interactions accounted for 6.8, 3.9, and 8.0% of the variation for S48M, S94M, and S95M, respectively. The trait with the lowest genotypic variance explained by genotype after yield was seed size with proportions of 45.0, 44.6, and 70.1% in S48M, S94M, and S95M, respectively; these values were still higher than the variance proportions for the G × Y interactions, which had values of 6.8, 11.0, and 8.6% for the three populations. Variation as a result of genotype for days to flowering was highly consistent across populations, with values of 89.0, 87.0, and 86.8% in S48M, S94M, and S95M, respectively. Lodging and maturity showed the highest variance proportion from G × Y interactions. Lodging had G × Y interaction values of 19.4, 27.0, and 23.6%, and maturity had values of 37.1, 28.3, and 27.4% for the S48M, S94M, and S95M populations, respectively. However, these values were still below those for genotypic variance proportions, which were 66.8, 72.9, and 74.2% for lodging and 36.4, 69.4, and 72.3% for maturity in populations S48M, S94M, and S95M, respectively.

Among the parents, Merlot, the adapted parent, was the highest yielding in both 2013 (2492 kg ha^{-1}) and 2014 (4065 kg ha^{-1}), resulting in a yield reduction of 39%. Among the SER lines, SER95 yielded the highest in both years with 1199 and 3157 kg ha^{-1}, respectively, equivalent to 62% reduction in yield. The geometric mean yield between the years showed that Merlot was the highest yielding parent with 3182 kg ha^{-1} followed by SER95 with 1946 kg ha^{-1}. The geometric mean yield of the RILs was 2511, 2695, and 2431 kg ha^{-1} for populations S48M, S94M, and S95M, respectively.

Transgressive segregation was observed for yield in both years. In 2013, the lines R13717 (from S48M) and R13627 (from S95M) yielded 3092 and 2936 kg ha^{-1}, significantly ($p < 0.05$) exceeded their best parent, Merlot, by ~600 kg ha^{-1}. In 2014, a total of 19 lines, all from S94M population, significantly ($p < 0.05$) outyielded Merlot. Line R13806 is the only genotype that yielded over the mean by two standard deviations in both years across all populations (Fig. 2). Yield reduction of 46% was observed for R13806 based on yield of 2811 and 5179 kg ha^{-1} in 2013 and 2014, respectively. A total of 60 lines significantly exceeded the geometric mean yield of Merlot, and the five lines with the highest geometric mean yields belonged to population S94M with the exception of R13627. The data from individual years and the geometric mean yield shows that relatively fewer lines maintained a high yield under drought conditions in 2013 with the exception of line R13717, while a greater proportion of lines excelled in performance under improved conditions in 2014. However, the geometric mean yield shows that about half of the best lines from different populations had favorable performance under both drought-stressed and nonstressed conditions.

The three SER parental lines performed well below the mean yields for both 2013 and 2014, as shown in Fig. 2, and their DSI were higher than Merlot and their respective RIL progeny. Despite their superior performance under drought and low-P conditions (Beebe et al., 2008) in tropical environments, the SER lines used in this study lacked adaptation to the temperate environment in Michigan (Fig 3a). The SER lines flowered and matured earlier (Fig. 3b; Table 1). SER94 showed the best overall adaptation to Michigan with values for flowering, maturity, and lodging most similar to Merlot among the SER lines. The best specific combining ability resulted from the SER94/Merlot cross as evidenced by the high geometric mean seed yield of the RILs in S94M in comparison with the other populations.

Broad-sense heritability estimates were obtained for all of the traits measured (Table 1). The H^2 estimates for seed yield were moderate to high, depending on the population, and values were 0.6, 0.8, and 0.8 for S48M, S94M, and S95M, respectively. Traits such as flowering and seed size resulted in high H^2 estimates across all populations (Table 2), whereas canopy height and lodging score resulted in moderate H^2 values in most populations. Days to maturity had moderate H^2 values in S94M (0.6) and S95M (0.6) and low values in S48M (0.1). Heritability estimates for wilting score were consistently low across all populations. Similar H^2 estimates for yield and phenology under drought stress were found in Ramirez-Vallejo and Kelly (1998) and for seed size in two pinto bean populations (Schneider et al., 1997).

Drought susceptibility indices based on seed yield resulted in higher DSI values of 1.3, 1.2, and 1.3 for SER48, SER94, and SER95 parents than Merlot, which had a DSI of 0.8. Previous reports have shown the superior performance of the SER lines included in this study among other lines from the same or different crosses under drought (Beebe et al., 2008). In our study, SER94 and

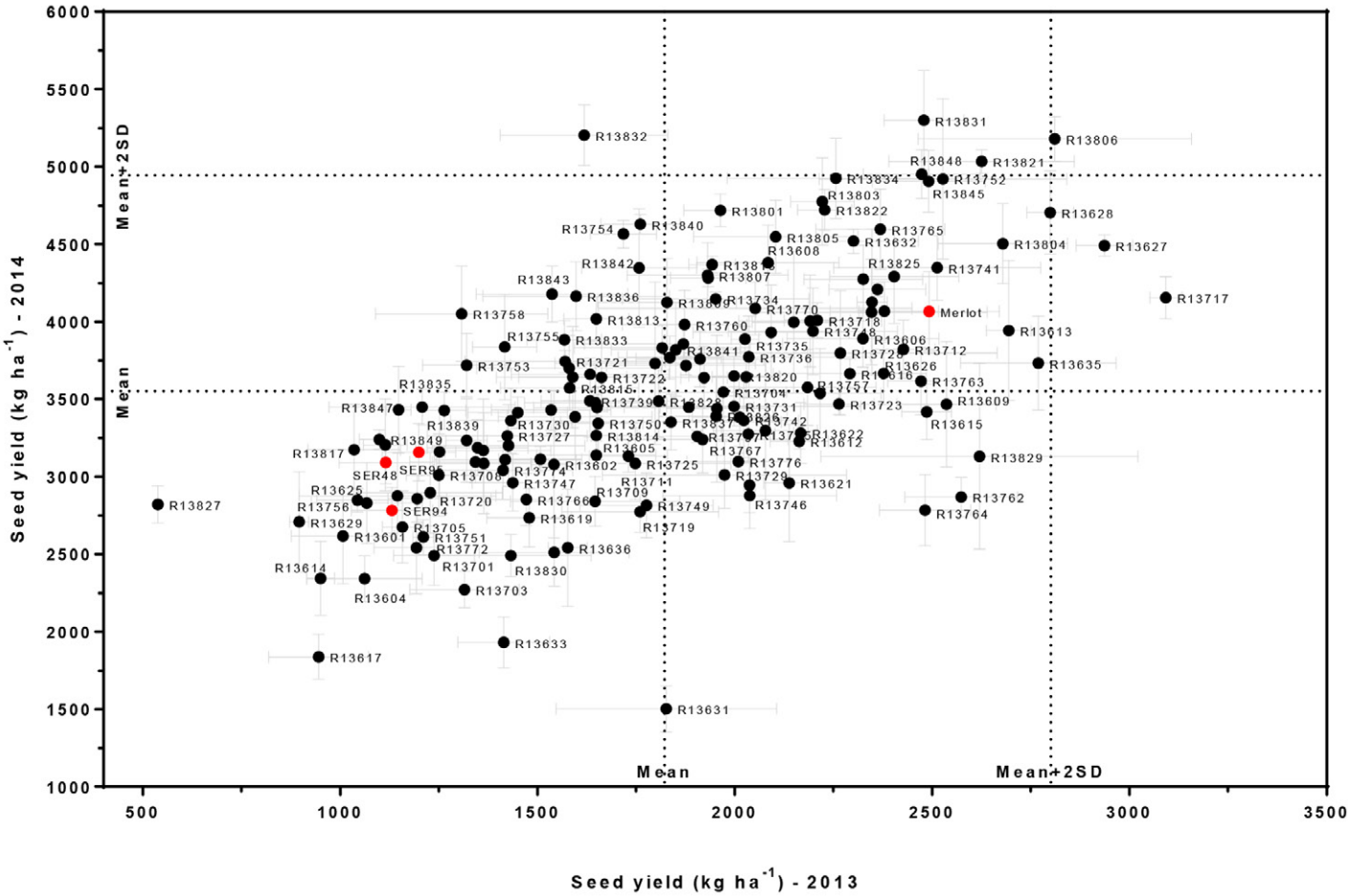

Fig. 2. Scatterplot of seed yield (kg ha^{-1}) between the 2013 (drought stress) and 2014 (unstressed) growing seasons for populations S48M, S94M, and S95M. Lines indicate the overall mean and the overall mean plus two standard deviations. Vertical and horizontal lines on each data point indicate standard errors for 2013 and 2014. Parents SER48, SER94, SER95, and 'Merlot' are identified in red.

SER95 produced similar yields within both stressed and unstressed conditions, which underscores the importance of local adaptation when selecting for drought tolerance. In contrast, SER48 had a difference of 491 kg ha^{-1} in 2013 and 871 kg ha^{-1} in 2014. From these values, it is evident that there was minimal difference in yield performance in SER94 between the trials in tropical locations and the Michigan trials. Significant genetic variation and low G × Y interaction coupled with high H^2 in traits, such as flowering, seed size, and canopy height, are useful indicators of the phenotypic stability and the underlying genetic nature of traits in common bean. Drought tolerance is often the result of selection for individuals that maximize phenology and yield components to match the adaptation to the target environment; it is widely known that local adaptation is important in developing drought-tolerant common bean cultivars (Beebe et al., 2013; White et al., 1994b).

Correlation analysis revealed a number of significant correlations among traits. Seed yield was correlated between years 2013 and 2014 ($r = 0.6$, $p < 0.05$) and negatively correlated ($r = -0.3$, $p < 0.05$) with wilting score in 2013. Seed yield was positively correlated with canopy height in 2013 ($r = 0.5$, $p < 0.05$) and 2014 ($r = 0.3$, $p < 0.05$). A negative correlation ($r = -0.54$ $p < 0.05$) between DSI and seed yield under drought (2013) was observed. Lodging and height were negatively correlated in 2014 ($r = -0.6$, $p < 0.05$) and with the geometric mean yield between years ($r = -0.4$, $p < 0.05$). Days to flowering and lodging were positively correlated in 2013 ($r = 0.3$, $p < 0.05$), 2014 ($r = 0.3$, $p < 0.05$) and with the geometric mean yield between years ($r = 0.4$, $p < 0.05$). Canopy height and seed yield are two commonly reported correlations in common bean. As expected, changes in plant architecture that favor pod placement away from contact with the soil reduce losses in yield from diseases and harvest losses when machine harvesting is used. Additional gains in yield from canopy height can also occur in type-II growth habit plants that produce pods along the length of the stem, and increased height provides more nodes for increased pod numbers (Kelly, 2001).

A significant negative correlation between wilting score and seed yield in a drought year suggests that wilting can be a useful surrogate measure of drought tolerance for the identification of superior lines. Studies in soybean [*Glycine max* (L.) Merr.] have also found wilting score as a feasible alternative for breeding programs

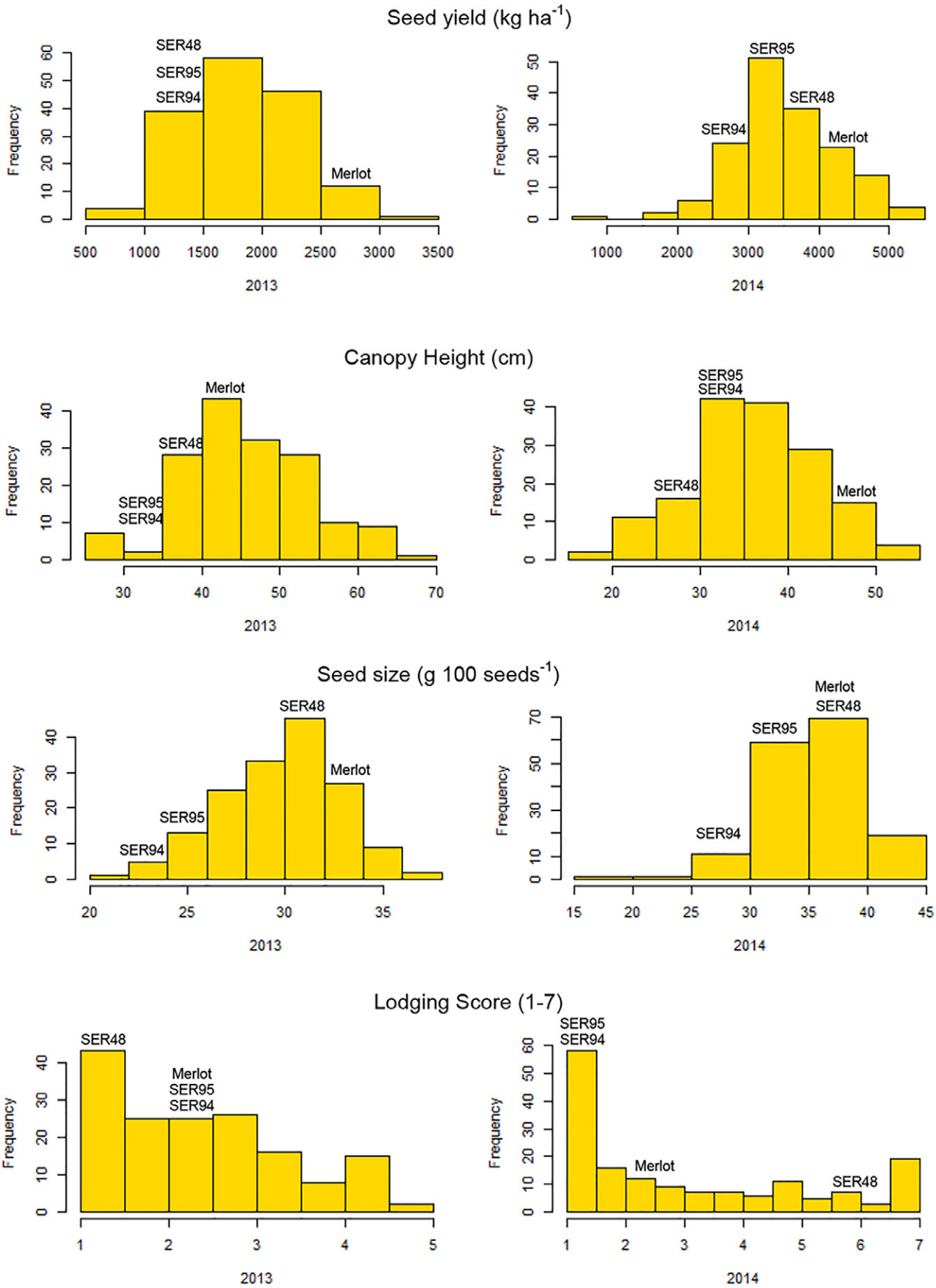

Fig. 3a. Histograms of seed yield, canopy height, seed size, and lodging score the S48M, S94M, and S95M populations during the 2013 and 2014 growing seasons in Michigan. Means of parents of each population are indicated by their names above the corresponding bin.

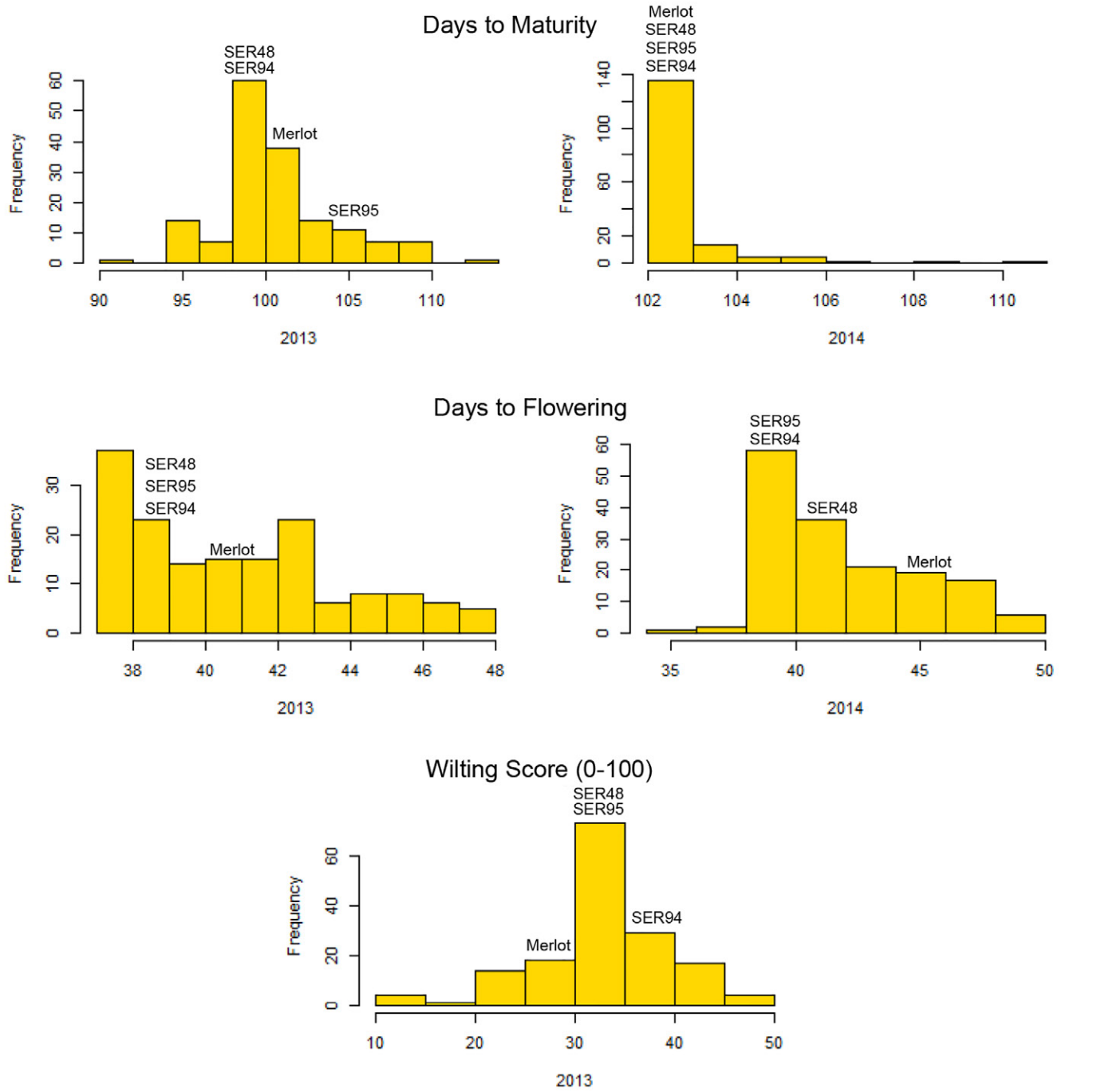

Fig. 3b. Histograms of days to maturity, days to flowering, and wilting score for the S48M, S94M, and S95M populations during the 2013 and 2014 growing seasons in Michigan. Means of parents of each population are indicated by their names above the corresponding bin.

to rapidly identify materials with superior breeding value for drought tolerance (King et al., 2009). Colocalization of QTL for wilting score, seed quality, and plant morphology and development have been reported (Charlson et al., 2009), while Pathan et al. (2014) identified soybean germplasm that exhibited slow wilting with reduced yield loss under drought. In common bean, Mukeshimana et al. (2014b) found significant negative correlation between wilting score and number of pods ($r = -0.63$) and dry biomass ($r = -0.72$) among other physiological parameters. This is also corroborated by the results of Ramirez-Vallejo and Kelly (1998) who identified a number of yield components and biomass traits associated with DSI.

Map Construction and Quantitative Trait Loci Mapping

The composite map of the three RIL populations provided greater genome and marker density than the individual map counterparts. A final set of 666 SNP markers were used to create the linkage map, covering a total of 909 cM. Of the initial 1046 polymorphic markers used, 33% were either identical or in segregation distortion, and

Table 2. Summary of quantitative trait loci (QTL) detected for seed yield, seed size, days to flowering, days to maturity, canopy height, and lodging score from the joint analysis of the S48M, S94M, and S95M populations grown at the Saginaw Valley Research and Extension Center, Richville, MI, in 2013 and 2014

Trait	QTL	Year	Chr.	Position	Interval	Marker interval	Joint LOD†	R^2‡	Additive effect§		
									S48M	S94M	S95M
				cM	Mb			%			
Seed yield (kg ha^{-1})	SY10.1	2013	Pv10	41	40.16–40.95	ss715646348–ss715645508	6.16	23.02	–178.77	–270.64	66.52
	SY3.3	2014	Pv03	53	37.06–45.59	ss715647671–ss715639244	4.09	30.79	–155.91	434.78	–24.79
	SY7.3	2014	Pv07	51	4.59–5.03	ss715650404–ss715640392	4.42	15.42	–197.46	–284.24	110.36
	SY7.4	2014	Pv07	68	37.47–38.83	ss715646778–ss715640271	4.70	18.80	–178.85	–312.78	168.10
	SY7.4	Combined	Pv07	67	30.15–37.47	ss715640138–ss715646778	3.59	17.00	–97.54	–213.47	178.88
Seed size (g 100 seeds^{-1})	SW8.3	2013	Pv08	51	3.14–6.65	ss715645829–ss715648043	3.83	16.44	–0.62	–1.67	–0.35
	SW9.3	2013	Pv09	22	16.72–16.98	ss715646842–ss715646451	3.97	20.22	0.19	–1.07	1.43
Days to flowering	DF1.2	2013	Pv01	51	42.44–42.85	ss715647282–ss715648652	4.49	17.13	0.02	–1.67	0.10
	DF1.2	2013	Pv01	62	43.7–47.79	ss715648889–ss715650192	4.18	12.46	–0.69	–1.43	–0.71
	DF1.1	2014	Pv01	47	36.58–40.31	ss715650565–ss715647891	8.57	36.15	–0.62	–2.73	–0.43
	DF1.3	Combined	Pv01	19	3.48–3.56	ss715648196–ss715648190	5.43	21.73	0.12	–1.82	0.07
	DF1.1	Combined	Pv01	40	15.67–15.64	ss715647050–ss715647049	7.02	27.39	0.03	–1.94	0.62
	DF1.2	Combined	Pv01	59	43.7–47.79	ss715648889–ss715650192	10.54	43.09	–0.66	–2.76	–0.54
Days to maturity	DM8.1	2014	Pv08	35	3.02–3.14	ss715645832–ss715645829	3.57	16.02	–0.03	–0.60	–0.35
Canopy height (cm)	HT10.1	2013	Pv010	44	40.99–41.2	ss715645510–ss715645524	3.77	17.00	–1.05	–3.74	2.38
Lodging score (1–7)	LDG7.1	2013	Pv07	86	45.88–46.7	ss715646613–ss715648553	4.44	11.81	0.30	0.36	0.48
	LDG7.2	2014	Pv07	84	48.63–45.98	ss715646609–ss715646525	4.16	10.30	0.05	0.87	0.47
	LDG1.1	Combined	Pv01	42	27.57–29.55	ss715649918–ss715646993	4.99	12.93	–0.54	–0.48	–0.01
	LDG7.1	Combined	Pv07	86	45.88–46.7	ss715646613–ss715648553	6.86	13.50	0.43	0.58	0.56

† LOD, logarithm of odds.

‡ R^2, broad-sense heritability; proportion of the phenotypic variance explained by the QTL at peak LOD.

§ Effect of allelic substitution in each population. Positive values indicate alleles from the common parent ('Merlot'); negative values indicate alleles from the noncommon SER 48, SER94, or SER95 parents.

thus were discarded from the analyses. The finalized composite map is shown in Supplemental Fig. S1. The shortest and longest map lengths estimated were 28.3 and 129 cM in chromosomes Pv04 and Pv02, respectively. The final map had well-distributed markers with an average distance between markers for the entire genome of 1.3 cM. Chromosomes Pv03 (2.62 cM) and Pv09 (2.48 cM) had the longest and Pv11 (0.68 cM) and Pv02 (0.82 cM) had the shortest average distances between markers. The composite map resulted in an improved version of the individual maps. This is explained by a number of indicators. First, individual maps for populations S95M, S48M, and S94M resulted in an average marker distance of 2.6, 5.0, and 3.6 cM, respectively, which is at least double that of the composite map. Second, the total numbers of markers used were 345, 106, and 399 for S48M, S94M, and S95M, respectively, or approximately half or less than the 666 markers used in the composite map. Third, the maximum distance between markers was 9.1, 5.8, and 3.8 cM for Pv03, Pv07, and Pv08 and in S48M, S94M and S95M, respectively. The total mapped distance was larger (1695.4 cM) in the S48M map than in the composite map, but this seemed to come at the cost of marker density with relatively large gaps in some chromosomes. The total map distances for individual S94M and S95M populations were 1061 and 380 cM, respectively. The use of a common parent reduced recombination biases while increasing QTL detection power.

A total of 14 QTL were found across the composite linkage map (Fig. 4). The JICIM mapping method proved useful in the detection of more QTL with more refined intervals than joint interval mapping. The use of the composite map using pooled segregation data also enhanced the power of detection of QTL that were otherwise questionable or not detectable using individual linkage maps for every population even though certain QTL were common among the two methods. Signals were detected for seed yield (2013, 2014, and combined), seed size (2013), days to flowering (2013, 2014, and combined), canopy height (2013), lodging score (2013, 2014, and combined), and days to maturity (2014). The QTL detection power generally improved in this study when LOD scores of individual maps were compared with the JICIM LOD scores using the composite map. For example, QTL SY10.1 on Pv10 had LOD scores of 0.1, 2.7, and 3.4 for S95M, S48M, and S94M, respectively, but the LOD score increased to 6.1 using the composite map and JICIM algorithm. A summary of these QTL is shown in Table 2.

Seed Yield

Four QTL (Fig. 4; Table 2) were found for yield on Pv03, Pv07, and Pv10; two were detected on Pv07 (2014 and combined); one on Pv03 (2014); and one on Pv10 (2013). The QTL for seed yield on Pv03 in 2014 was located between markers ss715647671 (37.0 Mb) and ss715639244 (45.5 Mb). This QTL had the largest R^2 of all the QTL for seed yield detected and the largest additive effect among all populations. The QTL SY7.3 on Pv07 in 2014 had a peak LOD of 4.4 and was found located between markers ss715650404 (4.5 Mb) and ss715640392 (5.0 Mb), which explained 15.4% of the variance. A second QTL, designated as SY7.4 in Pv07, was found in 2014 between markers ss715646778 (37.4 Mb) and ss715640271 (38.8 Mb) with an R^2 of 18.8%. This QTL was also found in the combined analysis with neighboring markers ss715640138 (30.1 Mb) and produced similar effects across populations. A fourth QTL was found on Pv10 in 2014 between markers ss715646348 (40.1 Mb) and ss715645508 (40.9 Mb). This QTL, SY10.1, had an R^2 of 23% and a peak LOD of 6.1. Cumulatively, the QTL found for seed yield accounted for 87.9% of the phenotypic variation, a value that approximates the heritability estimates across populations for seed yield. The interactions among the yield QTL would need to be analyzed and the R^2 recalculated to validate their additivity. A general examination of the additive effect reveals that out of the 12 independent (four QTL × three populations) additive effect estimates, eight correspond to alleles from the SER parents. However, the QTL SY3.3 with the single largest effect (435 kg ha^{-1}) among all populations was inherited from Merlot in S94M. Multiple QTL donated by the SER parents, especially in 2014, are a surprising result, as the SER lines were envisioned as the donors of drought tolerance and Merlot as the source of yield and agronomic performance.

Previous research has reported QTL for seed yield in Pv03, Pv07, and Pv10. In a 3-yr study of a black bean RIL population, Wright and Kelly (2011) found SY10.2 QTL on Pv10 and one QTL on Pv03 using simple-sequence repeat, sequence-related amplified polymorphism, target-region amplified polymorphism, and sequence-characterized amplified polymorphism markers. Blair et al. (2012) found four small-effect QTL in Pv03 (irrigated, 2 yr), one QTL in Pv07 (irrigated, 1 yr), and one in Pv10 (drought stress, 1 yr) in BAT477/DOR364 RIL population. Using the same population, Asfaw et al. (2012) found a QTL on Pv07 in a three-location study in Africa and Colombia evaluated under drought and nonstressed conditions. These results overlap with data reported here as SY10.1 was identified on a drought year (2013) and SY3.3, SY7.3, and SY7.4 were identified in the nonstress year (2014). The additive effects of SY7.3 reported here are also similar to the additive effect value reported in Blair et al. (2012). A search of the genes located within the SY10.1 interval resulted in 56 genes in a 0.7-Mb space; this list is included in Supplemental Table S1. Gene ontology enrichment analysis resulted in 11 significant molecular function ontology terms, with oxidoreductase activity, acting on single donors with incorporation of molecular oxygen, incorporation of two atoms of oxygen (12 genes) and lipoxygenase activity (11 genes) as the most significant terms.

With the recent release of the BARCBean6K_3 SNP array, Hoyos-Villegas et al. (2015) and Trapp et al. (2015) reported QTL for seed yield on Pv03 and Pv10. Trapp et al. (2015) used a 140-RIL population from the cross Buster/Roza evaluated for 2 yr under multiple drought and nonstress conditions in three locations. The QTL SY10.1, detected under drought conditions in Nebraska in 1 yr, is located at 39.9 Mb in Pv10 (Trapp et al., 2015) and is in proximity to SY10.1 in our study (40.1 Mb). Hoyos-Villegas et al. (2015) detected a QTL, SY 3.3, for seed yield on Pv03 when evaluated for 3 yr under high white mold pressure. Upon further inspection, ss715639244 SNP was found to be a significant marker located within the interval for SY3.3 that overlaps with the confidence interval of QTL SY3.3 reported here. The QTL SY3.3 resulted in a list of 710 genes in an 8.5-Mb genome distance (Supplemental Table S2); no significant GO terms were found among the genes for this QTL. In a 3-yr study using a RIL population derived from black bean Tacana and PI313850, Mkwaila et al. (2011) found QTL SY7.2 on Pv07 in 2 yr of the study. In a genome-wide association study (GWAS) to find markers associated with agronomic traits in the Andean Diversity Panel (Cichy et al., 2015), Kamfwa et al. (2015) found a significant SNP on Pv07 associated with pod number. This SNP (ss715647649) is located within the confidence interval for SY7.4 reported

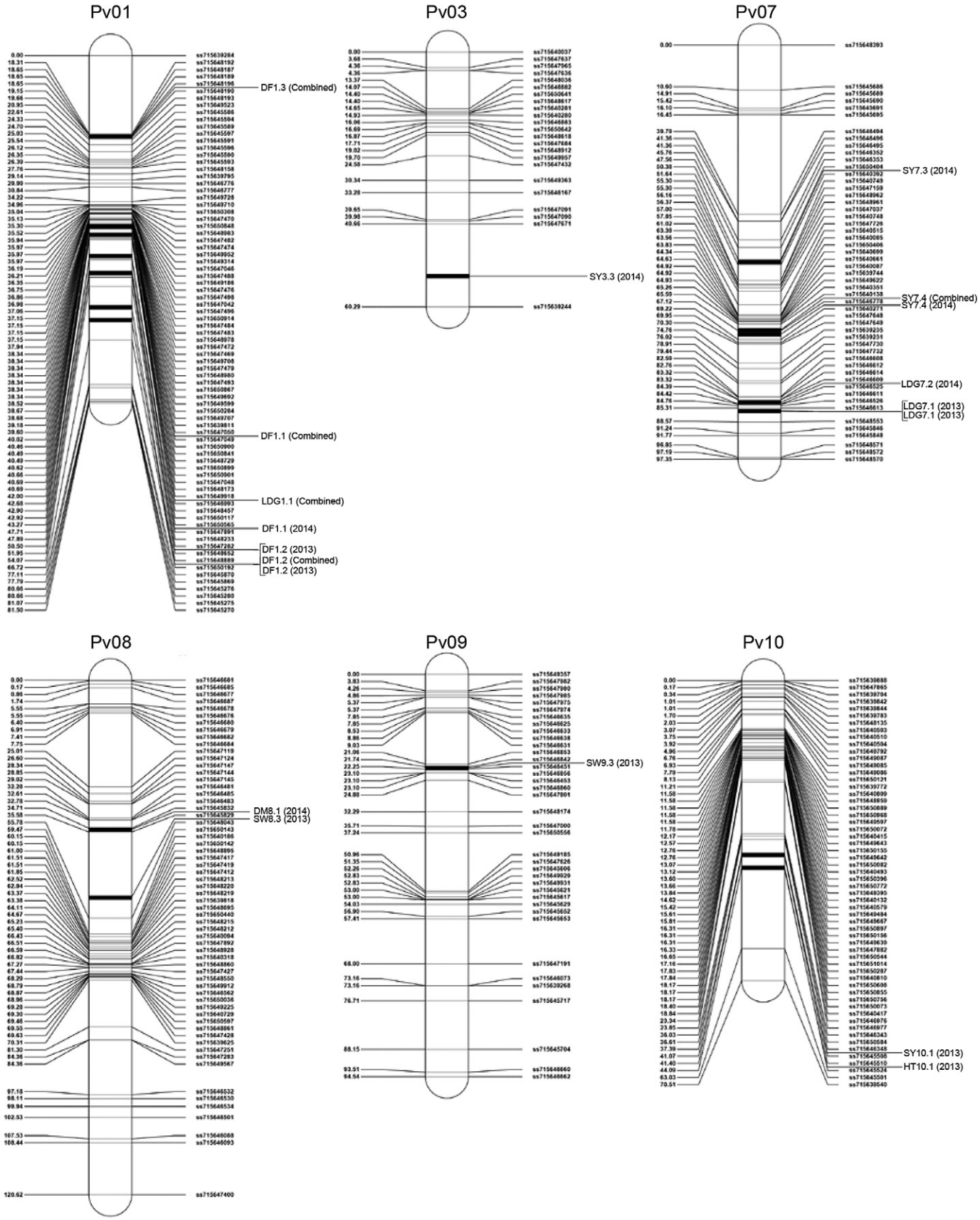

Fig. 4. Composite map of chromosomes Pv01, Pv03, Pv07, Pv08, Pv09, and Pv10 with quantitative trait loci detected for days to flowering (DF) on Pv01; lodging score (LDG) on Pv07; seed yield (SY) on Pv03, Pv07, and Pv10; days to maturity (DM) on Pv08; seed size (SW) on Pv08 and Pv09; and canopy height (HT) on Pv10 and their corresponding year or combined analyses.

in our study. A search for genes in the QTL SY7.3 interval found 38 genes (Supplemental Table S3) in a 0.4-Mb genome space. Gene ontology term analysis resulted in gene groups for the biological process and molecular function ontologies. Biological functions amine metabolic process (four genes) were the most significant group and organonitrogen compound metabolic process (six genes) were the second most significant group. Among the five molecular function ontology groups found, primary amine oxidase activity (four genes) and oxidoreductase activity, acting on the CH-NH_2 group of donors, oxygen as acceptor (four genes) resulted in the most significant groups. The QTL SY7.4 in 2014 resulted in 81 genes in a 1.3-Mb interval (Supplemental Table S4). A total of 223 genes were found for the combined analysis SY7.4 QTL (Supplemental Table S5) in a 7.3-Mb genome space. Significant GO biological processes were gas transport (six genes) and oxygen transport (six genes). The oxygen binding (six genes) resulted in a significant molecular function GO term for QTL SY7.4.

Seed Size

Two QTL for seed size were found in 2013 on Pv08 and Pv09 (Fig. 4; Table 2). The QTL on Pv08, designated as SW8.3, was located between markers ss715645829 (3.1 Mb) and ss715648043 (6.6 Mb). The QTL on Pv09 was designated as SW9.3 and was located between markers ss715646842 (16.7 Mb) and ss715646451 (16.9 Mb); this QTL had an R^2 of 20.2%. The QTL interval for SW8.3 contained a total of 347 genes and 26 SNPs, but no GO enrichment was found for any of the terms in this QTL (Supplemental Table S6). In contrast, SW9.3 resulted in a small set of genes contained within its interval (20 genes) that were also significantly grouped into cellular component and molecular function ontologies (Supplemental Table S7). The most significant cellular component was 6-phosphofructokinase complex (two genes), and phosphofructokinase activity and 6-phosphofructokinase activity were the most significant molecular functions with the same two genes in common (Phvul.009G112400 and Phvul.009G112500) within the groups.

The QTL for seed size in Pv08 and Pv09 have been found in previous studies in common bean. For example, Trapp et al. (2015) detected two QTL for seed size on Pv08 under nonstressed conditions in 2 yr of the study; this is consistent with our findings in that SW8.3 was also found in a nonstress year (Table 2). In a RIL population from the cross PC-50/XAN-159, Park et al. (2000) found a small-effect QTL for seed weight on Pv08. In a cross between the parents 'Xana' and 'Cornell 49242', Pérez-Vega et al. (2010) derived 104 RILs and found two QTL for seed weight on Pv08 designated as SW8.1 and SW8.2. Hoyos-Villegas et al. (2015) also detected two significant QTL for seed size on Pv08 using SNP markers; however, none of these markers showed overlap with the SNPs reported here. Blair et al. (2006) also detected two QTL for seed size on Pv08 and one on Pv09 on the same population where a QTL for seed yield was detected on Pv03 as described before. In a second population derived from DOR364/BAT477, Blair et al. (2012) found two QTL under drought conditions associated with seed size on Pv09, which is consistent with the detection of SW9.3 in a drought-stress year (2013).

Days to Flowering

Three QTL, DF1.1, DF1.2, and DF1.3, for days to flowering were found (Fig. 4; Table 2) on Pv01 in the years 2013, 2014, and the combined analysis. The DF1.1 QTL was located between SNPs ss715647050 (15.6 Mb) and ss715647049 (15.6 Mb) in the combined analysis. A second QTL, DF1.2, was detected between ss715648889 (43.7 Mb) and ss715650192 (47.7 Mb) in 2013 and in the combined analysis. A third QTL, designated as DF1.3, was found between SNPs ss715648196 (3.4 Mb) and ss715648190 (3.5 Mb), which resulted in an R^2 of 21.7%. The combined analysis revealed that QTL DF1.2 explained 43% of the variation for flowering with a LOD of 10.5 and was the most significant of all QTL reported among all traits in this study. A large additive effect could be attributed to QTL DF1.2, whereby the respective SER line parents contributed to −0.5, −0.6, and −2.7 d to flowering, respectively, because of the presence of this QTL. As with the seed yield QTL, the sum of the variance explained in the combined analysis among the QTL in these populations was 92.2% (Table 2). This value approximates the heritability calculated from mean squares estimates of days to flowering (S48M = 0.9, S94M = 0.8, and S95M = 0.8), which implies that QTL DF1.1, DF1.2, and DF1.3 explain almost all of the genetic variance present in these populations. This figure can also be corroborated by the sum of the maximum (S94M) additive effects of these three QTL, which results in ~6.5 d, a value that approximates the range for flowering across populations (Fig. 3b). In the cases where QTL had significant additive effects (>0.5 d), these were contributed by the early-flowering SER parental lines (Table 1; Fig. 3b).

Previous QTL mapping efforts have identified highly significant signals controlling days to flowering. Blair et al. (2006) detected a highly significant QTL for days to flowering on Pv01. Pérez-Vega et al. (2012) also detected a highly significant QTL for flowering on Pv01 and reported similar R^2 values to those reported here for DF1.2 (combined analysis) in an Andean–Mesoamerican cross. Finding the same QTL in contrasting genepool crosses suggests that flowering in both common bean genepools is largely controlled by the loci detected on Pv01. Trapp et al. (2015) also detected two QTL, DF1.1 and DF1.2, located at 3.3 and 47.7 cM, respectively. This

is consistent with our finding of DF1.3 (19 cM) and DF1.2 (59 cM) at opposite locations of both linkage maps. Further confirmation of both QTL are the common SNPs (ss715639811 and ss715646993) they share with DF1.1 and the four SNPs (ss715647046, ss715647050, ss715647049 and ss715649918) shared with DF1.2 reported by Hoyos-Villegas et al. (2015).

Gene queries for DF1.1, DF1.2, and DF1.3 resulted in different numbers of genes underlying the intervals (Supplemental Table S8–S13). DF1.2 in 2013 and the combined analysis returned the same number of genes (406 genes in a 4-Mb span), as they mapped to the same location. The closely located interval also designated DF1.2 in 2013 resulted in 38 genes in a 0.03-Mb space. The QTL DF1.1 in 2014 resulted in 209 genes in a 3.7-Mb distance. The combined analysis for DF1.1 and DF1.3 resulted in seven and one gene in 80- and 0.02-Mb distances, respectively. The annotation on the single gene found on the interval for the combined analysis of DF1.1 resulted in an endosomal targeting BRO1-like domain-containing protein gene as the closest match to the *A. thaliana* genome annotation. Gene ontology terms returned defense response (14 genes) and response to stress (18 genes) as the biological processes associated with DF1.1 in 2014 from the set of the genes submitted to the analysis (Supplemental Table S10). Likewise, a total of 17 molecular function GO terms were found for DF1.1 in 2014 as significant ($p < 0.05$) including ADP binding (14 genes) and organic cyclic compound binding (61 genes) as the most significant terms. The QTL DF1.2 in 2013 and the combined analyses also returned significant molecular function GO terms; a total of eight terms were found with ATPase activity (eight genes) and pectinesterase activity (12 genes) as the most significant.

Days to Maturity

One QTL, DM8.1, for days to maturity was detected on Pv08 in 2014 and is located between markers ss715645832 (3 Mb) and ss715645829 (3.1 Mb). This QTL (DM8.1), inherited by the SER parents, had a joint LOD of 3.5 and accounted for 16% of the variation, which resulted in an effect between −0.6 (S94M) and −0.35 (S95M). The interval for QTL DM8.1 contains 14 genes in a 0.1-Mb space. No significant GO enrichment was found for this set of genes (Supplemental Table S14). Trapp et al. (2015) found the same QTL HM8.1 for maturity under nonstressed conditions, which is in accordance with the QTL found in our study in a nonstressed year (2014).

Canopy Height

The QTL HT10.1 was detected in 2013 on Pv10 between markers ss715645510 (40.9 Mb) and ss715645524 (41.2 Mb) with a LOD of 3.7 and an R^2 of 17% (Fig. 4; Table 2). However, this only resulted in modest additive effects: −1, −3.7, and 2.3 cM in S48M, S94M, and S95M. A list with 24 genes in a 0.2-Mb span was retrieved from the interval for HT10.1 (Supplemental Table S15), but no GO enrichment was found for this set of genes. As no prior studies were found on height QTL on Pv10, we propose this QTL as HT10.1.

Lodging Score

Three QTL designated as LDG1.1 (combined), LDG7.1 (2014), and LDG7.2 (2013 and combined) were found on Pv01 and Pv07. The QTL LDG7.1 was found in the same interval between ss715646613 (45.8 Mb) and ss715648553 (45.7 Mb) and the R^2 for this QTL was ranged from 11.8 to 13.5% (. 4; Table 2). As expected, all QTL were inherited from Merlot, which was developed to exhibit improved plant architecture with resistance to lodging (Hosfield et al., 2004). The QTL LDG7.1 (2013 and combined) contained 80 genes in a 0.8-Mb genome space (Supplemental Table S16–S17), whereas LDG7.2 contained 262 genes in a 2.6-Mb space (Supplemental Table S18). The QTL LDG1.1 contained 22 genes in a 1.9-Mb space (Supplemental Table S19). In terms of GO enrichment analysis, LDG7.2 contains nine genes involved in the molecular function terms prenyltransferase activity or transferase activity, transferring alkyl or aryl (other than methyl) groups. Although the percentage variance explained by the QTL was not as high in our study, the additive effects were comparable between their two populations (approximately −0.4) and LDG7.1 (2013 and combined) across S48M, S94M, and S95M, (~0.3 to ~0.5). Kolkman and Kelly (2003) and Ender and Kelly (2005) detected QTL in Pv07 with similar R^2 and effect size (approximately −0.4) to LDG7.2 (2014). Mkwaila et al. (2011) also found QTL for lodging on Pv07 in two separate populations (Tacana/PI318695 and Tacana/PI313850) used for mapping of traits associated with white mold avoidance. In a separate study, Hoyos-Villegas (2015) found that a peak SNP (ss715646517) from a GWAS signal that is within the QTL interval for LDG7.1 and LDG7.2 and suggested an effect of −0.6 lodging score units associated with SNP ss715646518. The SNP ss715646517 was found to be in linkage disequilibrium ($r > 0.5$) with nine genes in a 0.1-Mb region. The genomic region that involved ss715646517 on Pv07 was on the exon of gene Phvul.007G222200, which is annotated with serine/threonine protein phosphatase.

CONCLUSIONS

In this study, we constructed three half-sib mapping populations between the cross of drought-tolerant SER48, SER94, and SER95 breeding lines from CIAT and the drought-susceptible cultivar Merlot from Michigan State University. Genotypic data based on SNP markers was used to construct a composite map of the three RIL mapping populations using pooled data. A total of 14 QTL were identified by means of JICIM using recombination

frequencies of markers across all populations. The use of these two elements increased our ability to detect small-effect QTL that were segregating in at least two of the populations but would not have been detected using individual linkage maps, in part, because of insufficient power associated with small population sizes. Joint inclusive composite interval mapping also allowed us to detect large- or moderate-effect QTL (particularly seed yield QTL SY10.1 and SY3.3) that were present in at least one of the populations. Because of the reproductive biology of common bean, large mapping populations (>150 individuals) are often difficult to generate. With the use of half-sib RIL populations, composite maps, and JICIM, QTL mapping projects can take advantage of increased detection power because of a larger number of individuals provided that the genetic effect of the QTL in question are sufficiently large and segregate among the families. To our knowledge, this is the first report that combines the use of a composite linkage map from a small NAM design and the use of the JICIM algorithm in common bean.

Supplemental Information Available

Supplemental information is available with the online version of this manuscript.

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