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RESEARCH

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ABSTRACT

Terminal and intermittent drought limits dry bean (*Phaseolus vulgaris* L.) production worldwide. Tolerance to drought exists but is difficult to breed for because of inconsistent expression across environments. Our objective was to identify quantitative trait loci (QTL) conditioning yield in a recombinant inbred line (RIL) population with consistent expression across multiple drought-stress environments. We tested 140 RILs from 'Buster' pinto (susceptible)/'Roza' pink (tolerant) for yield under multiple stresses (intermittent drought, compaction, and low fertility) across 3 yr and terminal drought across four location-years. A genetic linkage map (953 cM) was generated using single nucleotide polymorphism (SNP) markers. Two major-effect QTL were detected on Pv01 and Pv02. The Pv01 QTL, defined by the closest marker SNP50809 (47.7 Mb), explained up to 37% of the phenotypic variance for seed yield under multiple stress (including intermittent drought) and was consistently expressed each year. The Pv02 QTL, nearest SNP40055 (11.8 Mb), was detected under drought stress (R^2 = 33%) in addition to multiple stress (R^2 = 17–23%). Phenological traits cosegregated with the yield QTL and affirmed the importance of phenological plasticity in adaptation to drought stress. Late maturity contributed to increased yield under multiple and nonstress and early maturity to increased yield under terminal drought. Given major and consistent effect, further investigation of the potential for the Pv01 and Pv02 QTL in breeding for multiple abiotic stress and drought tolerance in dry bean is warranted.

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Abbreviations: BLUP, best linear unbiased predictor; BR, 'Buster'/'Roza' cross; DF, days to flowering; DII, drought intensity index; DS, drought stress (treatment); DSF, days to seed fill; DSI, drought stress index; GE, genotype-by-environment interaction; GM, geometric mean; HM, days to harvest maturity; LOD, logarithm of odds; MAS, marker-assisted selection; MS, multiple stress (treatment); NS, nonstress (treatment); PR, percentage yield reduction; QTL, quantitative trait loci; RIL, recombinant inbred line; SNP, single nucleotide polymorphism; SW, 100-seed weight; SY, seed yield.

Drought is a major constraint limiting dry bean yield worldwide. The Mexican highlands and northeastern Brazil both produce over one million hectares of beans and can have yields that fall below 0.4 t ha^{-1} (Beebe et al., 2010) due to limited water. The United States is also a leader in dry bean production and over half of its acreage is grown under rainfed conditions that are increasingly susceptible to intermittent drought. The western region of the United States maintains dry bean production under irrigation, and, due to water shortage and costs associated with water use, there is a potential shift to limited irrigation systems that are prone to intermittent drought stress. Terminal drought occurs in many countries, particularly the lowland tropics, which plant beans during the rainy season. Often, the rains cease before

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the crop is filled, resulting in insufficient water toward the end of their reproductive growth (Frahm et al., 2004). To address intermittent and terminal drought issues, breeders are increasing efforts to improve genetic gains of dry bean under water-limited conditions (Beebe et al., 2010), and dry bean breeding programs in Michigan, Idaho, and Nebraska have focused breeding efforts on drought tolerance (Ramirez-Vallejo and Kelly, 1998; Singh, 2007; Urrea et al., 2009). Drought-tolerant lines developed for tropical environments are used in commercial production (Teran and Singh, 2002; Beebe et al., 2010). While drought-tolerant lines have been developed via traditional breeding methods, a great potential exists for marker-assisted breeding to accelerate drought tolerance breeding.

Drought stress manifests differently due to the timing, duration, and intensity of the limiting water stress and can be amplified by other stresses such as poor soils, disease, and heat (Blum, 2011). Many plant traits influence tolerance to drought stress including rooting pattern (Sponchiado et al., 1989; Beebe et al., 2007), capacity to partition a greater proportion of carbohydrate to seed under stress (Rao, 2001), capacity to set pods and fill seeds under stress (Ramirez-Vallejo and Kelly, 1998; Beebe et al., 2007; Singh, 2007), reduced stomatal conductance and leaf area, and the capability to maintain turgor through osmotic adjustment (Beebe et al., 2010). Selection for grain yield under stress provides the best opportunity for improving tolerance to abiotic stress via traditional breeding (Frahm et al., 2004; Muñoz-Perea et al., 2006; Beebe et al., 2007). Terán and Singh (2002) reported that race Durango germplasm from the semiarid highlands of Mexico possessed the best drought tolerance among landrace germplasm, but that even better lines were derived from a double cross combining race Durango and race Mesoamerica germplasm. Roza pink bean, which is derived from a similar interracial cross (Burke, 1982), exhibits drought-stress tolerance in the Pacific Northwest. 'Pinto Villa', 'Pinto Saltillo' (Acosta-Gallegos et al., 1995; Sánchez-Valdez et al., 2004), and SEA 5 (Singh et al., 2001; Terán and Singh, 2002) represent additional Durango germplasm identified with drought tolerance.

Breeding for drought is complex due to number of traits involved, quantitative inheritance, and environmental influence (Mir et al., 2012). The potential to select for drought tolerance via marker-assisted selection (MAS) was investigated by Schneider et al. (1997). They observed that genotype-by-environment interaction affected the expression of identified QTL such that potential for MAS in breeding for drought tolerance was inconclusive. Beebe et al. (2007) identified QTL for yield under drought using a RIL population (SEA 5/MD 23-24), which also influenced yield in well-watered environments, suggesting that yield under both conditions could be combined. Recent evidence indicates that selection for drought tolerance will improve tolerance to low P (Beebe et al., 2008). This putative association of low-soil-fertility tolerance with drought tolerance warrants further study in temperate environments. Asfaw et al. (2012) tagged significant QTL related to photosynthate remobilization but found that the QTL explained low total genetic variance. These efforts have generated a large amount of data that has contributed to understanding the impact of drought on dry bean; however, the identification of major-effect QTL with stable expression across different stress environments is needed to facilitate MAS for tolerance to drought stress in bean. The objective of the current study was to identify and validate major-effect QTL in dry bean with stable expression across different drought stress environments using a biparental inbred population.

MATERIALS AND METHODS

Plant Material

A mapping population from the cross Buster/Roza (BR), consisting of 140 $F_{7:9}$ RILs, was developed using the single-seed-descent method beginning with the F_2 generation. Roza pink bean originates from a multiple-stress nursery located on the Washington State University, Research Farm Unit near Prosser, WA (Burke, 1982). Also known as the "purgatory plot," this field is characterized by compacted soil, no supplemental fertilizer, a water deficit of at least 30%, and a high population of *Fusarium solani* pv *phaseoli* (*Fsp*) causing Fusarium root rot disease. Roza was developed from a cross between 'Red Mexican UI-35'//P.I. 203958/'Sutter Pink'. From this cross, Roza has moderate tolerance to drought from Sutter Pink (Durango race), *Beet curly top virus* and *Bean common mosaic virus* resistance from Red Mexican UI-35 (Durango race); P.I. 203958 (Mesoamerican race) contributed tolerance to *Fsp* (Burke, 1982). Roza has an indeterminate-prostrate type III growth habit (Schoonhoven and Pastor-Corrales, 1987). Buster pinto (from a private seed company) has an indeterminate short-vine and upright type IIb growth habit. Buster was chosen as a parent for this study because it performed poorly compared to Roza in the multiple-stress purgatory plot from 2002 to 2006. Otherwise, Buster yielded comparable to Roza under nonstress conditions at the Washington State University, Research Farm in Othello, WA (Trapp et al., 2012).

Field Conditions and Phenotyping

Multiple Stress Site

In 2006, 2007, and 2008, experiments under multiple stress (MS) were conducted on the purgatory plot at the Washington State University, Research Farm, Prosser, WA, which is located at 46°29′ N and −119°73′ W and has a Warden (coarse-silty, mixed, superactive, mesic Xeric Haplocambids) soil type. An average rainfall of 51 mm (Hoogenboom, 2014) and mean temperature of 20.6°C during the growing season (May–August) provides exceptional conditions for drought-tolerance testing. Each year, 140 BR RILs, the parents, and 'Othello' pinto as a check, were planted in a randomized complete block design with three replications. Trials were planted mid- to late May.

A plot consisted of one row with 3-m length. A spacing of 0.6 m between rows was used. Target seeding rate was 285,000 plants ha^{-1}. Due to space limitations, only the stress treatment was planted in 2006 and 2007; however, there were two treatments (stress and nonstress) sown in 2008. Multiple stress was generated by compacted soils due to reduced tillage practices, low soil fertility (<10 mg kg^{-1} P and <30 kg ha^{-1} available N), and intermittent drought stress imposed by only applying approximately 25 mm of water by overhead irrigation via hand lines every 8 to 10 d post stand establishment at the V3 to V4 vegetative growth stages (Schwartz and Langham, 2010). This represented about 30% of the rate of evapotranspiration during the same time period (Hoogenboom, 2014). Yield (kg ha^{-1}) was the only trait obtained from the MS trials.

Drought Stress Sites

Terminal drought-stress trials were conducted at the Washington State University, Research Farm in Othello, WA and University of Nebraska, Research Station in Mitchell, NE, for 2 yr (2011 and 2012). Othello, WA is located at 46°49′ N and −119°10′ W and has a Shano (coarse-silty, mixed, superactive, mesic, Xeric Haplocambid) soil type. The average rainfall is 64 mm and mean temperature is 20°C during the growing season. Mitchell, NE, located at 41°56.6′ N, −103°41.9′ W, has a Mitchell (coarse-silty, mixed, superactive, calcareous, mesic, Ustic Torriorthent) soil type, an average rainfall of 203 mm and a mean temperature of 19°C during the growing season. Each experiment consisted of 140 RILs, both parents, and Othello pinto as a check, with two replications and two treatments, drought stress (DS) and nonstress (NS) in a 12-by-12 lattice split plot (with stress as the main plot and lines as the subplots) design planted in early June. For Washington trials, lines were planted in four-row plots with 3-m length and 0.6-m row spacing. For the Nebraska trials, lines were planted in two-row plots with 7.6-m length and 0.6-m row spacing.

Trials at both locations used furrow irrigation. Both treatments were watered on a regular watering schedule until flowering (R1 growth stage) when terminal drought was simulated by ceasing irrigation on the DS treatment. Conversely, the NS plots received four to six more irrigations after flowering. Four- and eight-row buffers were planted the length of the field between treatment main plots to reduce the lateral movement of irrigation water between the NS and DS plots. Soil water content was measured in Washington (neutron probe) and Nebraska (Watermark probe, Spectrum Technologies) at three depths (22, 45, and 75 cm below the soil surface) three times during the growing season: after the first water to determine field capacity (R1), at midpod fill (R4–5), and at harvest maturity (R9). Probes were placed within each replication of the parental plots Roza and Buster. The neutron-probe measurement is based on the amount of hydrogen ions in the soil and reported herein as centimeters, whereas the Watermark probe is associated with soil water tension and the resistance detected is measured in kilopascals (kPa).

The number of days to flowering (DF), harvest maturity (HM), and seed fill (DSF; DSF = HM − DF), 100-seed weight (SW; g 100 $seeds^{-1}$), and yield (kg ha^{-1}) were obtained. Percentage yield reduction (PR), geometric mean [GM; $GM = \sqrt{(Y_s \times Y_i)}$] where Y_s is the mean seed yield (SY) of a line under DS and Y_i is the mean yield of the line under NS (Schneider et al., 1997), drought intensity index (DII; $DII = 1 - X_d/X_p$) where X_d is mean yield averaged across lines under DS and X_p is mean yield under NS, and drought stress index [DSI; $DSI = (1 - Y_d/Y_p)/DII$] where Y_d is mean yield of a line under DS and Y_p is mean yield for the same line under NS (Fischer and Maurer, 1978) were also calculated. Percentage yield reduction, GM, and DSI were used in QTL analysis.

Statistical Analyses

Best linear unbiased predictors (BLUPs) were determined for all traits for combined analyses and in single environments using the restricted maximum likelihood procedure in PROC MIXED (SAS Institute, 2011). The MS trials were combined across 3 yr and analyzed separately from the terminal drought trials, which were combined across four location-years. Genotype, environment, replication, and blocks were fitted as random effects and treatment as a fixed effect. Phenotypic correlations between pairs of traits were calculated with means from the combined analyses using the PROC CORR Spearman procedure of SAS. The trait means for the DS and NS treatments are reported separately. Correlations between mean yield from the MS trial with the trait means from the terminal drought trial were also conducted. Associations of significant SNP markers with specific traits were confirmed using simple and multiple regression analysis (PROC REG).

DNA Preparation and Genotyping

Genomic DNA was extracted from the emerging trifoliate leaf for each RIL and parent. Total genomic DNA was isolated using the FastDNA SPIN Kit (MP Biomedicals, LLC) according to the manufacturer's instructions. DNA concentration was determined by a ND-1000 spectrophotometer (Thermo Fisher Scientific) and diluted to 50 ng μL^{-1}. The BARCBean6K_3 BeadChip (Viteri et al., 2014) with 5398 SNPs was used to genotype Buster, Roza, and the 140 RILs. The SNP assay was conducted on the Illumina platform following the Infinium HD Assay Ultra Protocol (Illumina, Inc.). Single nucleotide polymorphism allele calling was completed using the GenomeStudio Genotyping Module v1.8.4 (Illumina, Inc.).

Mapping and Quantitative Trait Loci Analyses

A genetic linkage map was constructed using JoinMap v.4.0 (Van Ooijen, 2006) set to Haldane's mapping function and default settings. Linkage groups were selected based on an independence logarithm of odds (LOD) score greater than 5. The linkage groups were aligned with the 11 chromosomes (Pv01 to Pv11) of the common bean genome based on physical map position of linked SNPs. The physical map location of the SNP markers was in reference to the 1.0 version of the whole-genome *P. vulgaris* map (Goodstein et al., 2012; Schmutz et al., 2014). The QTL analysis was conducted using composite interval mapping with QGene 4.0 (Joehanes and Nelson, 2008). A permutation test (1000 permutations) was used to set a significant QTL threshold at the 0.01 level of probability to determine the significant LOD level for declaration of a QTL. Estimates of the phenotypic variation (R^2) explained by the individual QTL,

Table 1. Average climatic conditions for seven location-years from May thru September including maximum, minimum, and average temperatures (°C), the number of days exceeding 35°C, total precipitation (mm), amount of precipitation from days after planting (DAP) until days to flowering (DF) and DF to harvest maturity (HM), and drought intensity index (DII).

Location	Year	Temperature			No. days max >35°C	Precipitation			DII
		Max	Min	Ave		Total	DAP to DF	DF to HM	
		°C			d	mm			
Prosser, WA	2006	38.1	3.8	18.9	3	21.6	2.8	18.8	NA
	2007	36.2	3.3	18.3	2	29.5	18.3	11.2	NA
	2008	37.8	4.6	18.5	5	31.8	23.9	7.9	0.4
Othello, WA	2011	33.9	2.3	17.4	0	47.2	37.6	9.7	0.5
	2012	39.9	3.3	18.4	6	16.5	16.5	0.0	0.2
Mitchell, NE	2011	26.7	10.8	18.7	0	252.5	239.3	13.2	0.5
	2012	29.6	12.0	20.8	0	75.2	53.6	21.6	0.4

and the effect of substituting one allele for the other were also determined in QGene. The marker within the QTL peak with the highest R^2 and $p \leq 0.01$ was used to define the genomic position of the QTL. Identified QTL were named according to Miklas and Porch (2010). For example, $SY1.1^{BR}$ represents a QTL for SY on chromosome Pv01 in the BR RIL population. Going forward, the BR superscript will distinguish among QTL identified for the same trait in different populations.

RESULTS

Climatic Conditions

Low precipitation across the seven separate trials provided the opportunity to develop drought stress by limiting or terminating irrigation (Table 1). The majority of the rainfall from May thru September occurred before flowering. Although the precipitation at the Nebraska site exceeded 250 mm during the growing season in 2011, the majority (200 mm) occurred before flowering and a moderate drought stress was achieved. The drought stress was more severe in 2011 compared to 2012 as reflected by the DII. The 0.2 DII for Washington in 2012 is attributable to unforeseen subsurface water source or leaching across the DS treatment. Neutron probe and Watermark data also show less soil moisture in 2011 vs. 2012 (Table 2). The high reading from Nebraska 2012 data indicates a probe malfunction in the Roza plot at 75 cm.

Multiple Stress Trials

Roza yielded 58% more than Buster under MS on the purgatory plot in Prosser, WA, for all 3 yr (Table 3). There was no significant difference in yield between Buster (4167 kg ha^{-1}) and Roza (4154 kg ha^{-1}) under NS in 2008. The mean yield for the RIL population also significantly differed between the two treatments in 2008 resulting in a comparable 0.4 DII (or stress intensity index). There was a significant genotype-by-environment interaction (GE) for the data combined across years (Table 5). Lack of complimentary NS experiments in 2006 and 2007 made it difficult to investigate potential factors causing the significant GE. But less stress in 2008 compared to 2006 and 2007 as indicated by greater average yield performance 2613 vs. 1529 and 1526 kg ha^{-1}, respectively, was likely a contributing factor. Nonetheless, most of the variance was attributed to genotype (44.2%) vs. GE (5.8%); therefore, data from the three MS trials were pooled and reported across years.

Table 2. Average soil moisture content for the plots with 'Buster'/'Roza' under optimum nonstress (NS) and terminal drought stress (DS) treatments for Othello, WA, (cm) and Mitchell, NE, (kPa) in 2011 and 2012.

Time†	Depth	2011 line (treatment)		2012 line (treatment)	
		Buster	Roza	Buster	Roza
	cm	NS/DS			
Othello, WA					
1	22	5.1/5.9	6.5/5.7	4.3/4.9	6.5/5.7
	45	4.1/4.3	4.3/4	3.5/3.9	4/3.9
	75	4.3/4.4	4.5/4.2	3.9/4.3	4.2/4.3
2	22	3.5/1.2	3.5/1.2	3.2/2.7	5.4/2.5
	45	3.9/2.6	4/2.2	3.8/4.4	4.5/3.8
	75	4.5/3.6	4.2/3.1	4.5/4.6	5.1/5
3	22	4.8/1.6	4.5/2.2	6.2/3.4	6.2/3.6
	45	4.1/2.3	3.7/1.9	4.7/4.5	5/4
	75	4.3/2.9	4.2/2.2	4.9/5.2	5.2/4.6
Mitchell, NE					
1‡	22	18.9/27.8	20.3/23.6	–	–
	45	19.5/22.1	23.9/25.4	–	–
	75	17.6/19.0	19.3/23.0	–	–
2	22	14.7/98.8	15.4/122.9	28.1/40.9	18.5/32.0
	45	15.2/47.3	23.4/112.8	26.2/31.8	21.4/35.1
	75	15.9/44.8	29.5/109.9	7.9/31.4	102.3/82.6
3	22	16.8/124.5	18.3/171.5	34.0/173.7	29.0/166.3
	45	16.5/43.2	21.0/131.8	30.1/120.8	27.0/117.2
	75	15.6/138.5	19.1/154.5	21.5/139.6	152.9/84.6

† Time 1 = plant stage V3/V4; Time 2 = R4; Time 3 = R8.

‡ Time 1 data is unavailable for Nebraska 2012.

Drought Stress versus Nonstress Trials

The data from the four terminal drought stress trials were evaluated first in the combined analysis and then as single environments primarily to examine robustness of QTL expression across locations and years. The DS and

Table 3. Means from single environments and across location-years for four traits measured in the 'Buster'/'Roza' recombinant inbred line (RIL) population including treatment (*T*), genotype × treatment (GT), and genotype × environment (GE) effects for single and combined environments.

				Parents		RIL Population						RILs Check
Trait	Year	Location	Trt†	Buster	Roza	Mean	Range	Genotype‡	*T*	GT	GE	(Othello)
Yield (kg ha^{-1})	Comb‡	Prosser	MS	1493	3555	2113	608–3935	***			***	1485
	2006	Prosser	MS	170	3641	1529	0–4320	***				647
	2007	Prosser	MS	1365	2930	1526	391–3948	***				1350
	2008	Prosser	MS	2875	3915	2613	995–4684	***	***	***		2392
			NS	4167	4154	4170	2291–6078	***				4378
	Comb	WA–NE	DS	2636	3898	2944	1283–4066	***	***	***	***	2488
			NS	5008	5830	4673	2946–6028	***				4412
	2011	WA	DS	2116	4172	2773	899–4513	***	*	*		1440
			NS	5173	5738	5197	2713–6804	***				3323
		NE	DS	753	1071	818	243–1369	***	ns	***		859
			NS	1745	2203	1713	915–2439	***				1739
	2012	WA	DS	3580	5092	3971	1809–5763	***	ns	*		3732
			NS	5053	6098	4878	5763–6650	**				3906
		NE	DS	3172	3761	3150	1353–4847	ns	**	ns		2895
			NS	5435	5520	4999	1957–7253	ns				5741
Seed weight (g 100 seeds^{-1})	Comb	WA–NE	DS	42	30	37	29–45	***	**	***	***	35
			NS	43	33	40	30–49	***				39
	2011	WA	DS	41	30	38	28–48	***	ns	***		33
			NS	45	40	42	32–54	***				41
		NE	DS	41	28	36	27–48	***	ns	***		36
			NS	42	31	39	29–51	***				40
	2012	WA	DS	47	40	40	29–50	***	ns	*		37
			NS	44	38	39	29–50	***				38
		NE	DS	39	31	35	26–43	***	ns	ns		32
			NS	42	33	39	20–48	***				40
Days to flowering	Comb	WA–NE	DS	47	50	48	44–55	***	ns	ns	***	42
			NS	46	49	48	44–54	***				43
	2011	WA	DS	49	50	51	39–58	***	ns	ns		39
			NS	49	50	51	40–56	***				40
		NE	DS	48	52	48	43–52	***	ns	ns		43
			NS	47	50	48	45–54	***				43
	2012	WA	DS	46	50	48	41–59	***	ns	ns		44
			NS	47	48	48	41–62	***				44
		NE	DS	43	47	45	41–48	***	ns	ns		42
			NS	43	48	45	40–48	ns				42
Days to harvest	Comb	WA–NE	DS	96	96	94	82–105	***	***	***	***	82
			NS	99	104	97	85–108	***				87
	2011	WA	DS	91	92	93	83–105	***	***	*		83
			NS	99	101	100	86–109	***				86
		NE	DS	102	105	98	78–108	***	ns	**		81
			NS	94	107	95	83–105	***				83
	2012	WA	DS	104	105	102	84–123	ns	ns	***		85
			NS	105	111	106	85–121	ns				89
		NE	DS	87	84	98	75–92	***	ns	ns		75
			NS	90	95	95	82–95	ns				85

(cont'd.)

NS treatments were analyzed separately. In the combined analysis, drought-tolerant Roza yielded 47% more than Buster under DS and both parents obtained similar yield under NS (Table 3). Yield of the RIL population ranged from 1283 to 4066 kg ha^{-1} for DS treatment and 2946 to 6028 kg ha^{-1} for NS. There was a significant treatment effect for all traits in the combined analysis with the exception of DF. This was expected as the water stress was not imposed until after flowering. One factor likely contributing to the significant GE for combined yield was the difference in drought severity between locations in 2012 (Washington DII = 0.2 and Nebraska = 0.4). For single

Table 3. Continued.

Trait	Year	Location	Trt†	Parents		RIL Population						RILs Check
				Buster	Roza	Mean	Range	Genotype‡	*T*	GT	GE	(Othello)
Days to seed fill	Comb	WA–NE	DS	49	46	44	33–52	***	ns	ns	ns	40
			NS	53	55	47	39–55	***				44
	2011	WA	DS	42	42	42	36–51	***	**	**		43
			NS	50	51	49	44–52	***				46
		NE	DS	55	54	51	30–61	***	***	**		38
			NS	47	56	47	36–58	***				40
	2012	WA	DS	58	56	54	39–67	***	ns	**		41
			NS	58	59	58	43–73	***				45
		NE	DS	44	37	40	31–49	***	*	ns		33
			NS	47	47	44	37–53	***				43

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

† Trt, treatment; MS, multiple stress; NS, well-watered nonstress; DS, drought stress.

‡ Comb, combined years under multiple stress when location is Prosser and combined years and locations under DS and NS when location is Washington and Nebraska (WA–NE).

§ ns, nonsignificant.

Table 4. Single nucleotide polymorphism marker coverage and distribution across the eleven chromosomes of common bean in Buster/Roza recombinant inbred line population.

Chromosome	Number of markers	Length	Average distance between markers
		cM	
Pv01	42	66.8	1.59
Pv02	56	97.2	1.74
Pv03	15	134.7	8.98
Pv04	21	71.7	3.41
Pv05	42	111.7	2.66
Pv06	37	70.7	1.91
Pv07	44	90.2	2.05
Pv08	31	104.8	3.38
Pv09	24	71.7	2.99
Pv10	28	103	3.68
Pv11	44	30.6	0.70
Entire Map	384	953.1	2.48

environments, mean yield was lower for DS than for NS treatments for all locations and years. The treatment effect was not significant ($p > 0.05$) at the Nebraska site in 2012 despite a DII of 0.4. The parents did not differ significantly within treatments at Nebraska both years.

QTL Mapping

A total of 1603 SNPs were used for mapping based on polymorphism, lack of genetic distortion, and <5% missing data. Of these, and after omitting SNP markers that mapped to the same location, 384 SNP markers were mapped across 11 chromosomes covering 953 cM (Table 4). Two major QTL were detected for yield under multiple stress in the purgatory plot. The QTL for yield on Pv01, tagged by SNP50809, was named SY1.1^{BR} (Table 5). This major QTL exhibited consistent expression under multiple stress each year (R^2 = 27.8–32.2) and was detected in the combined analysis (R^2 = 36.8). The same QTL was detected in a few of the terminal drought trials specifically under NS in Washington 2011 (R^2 = 12.5) and Nebraska 2012 (R^2 = 8.3). Major QTL for other traits colocated with SY1.1, namely DF (DF1.2^{BR}) and HM (HM1.1^{BR}). DF1.2 was detected in the combined analysis (R^2 = 55.3) and single location-years (R^2 = 27.3–53.6), and HM1.1 in single location-years (R^2 = 11.8 to 16.0). Minor-effect QTL for SW (SW2.2^{BR}) and DSF1.1^{BR} also colocated with SY1.1.

The second major QTL (SY2.1^{BR}) for yield under multiple stress was detected on Pv02 (R^2 = 16.7–22.7). SY2.1 was also detected in the terminal drought trials, but specifically in the DS treatment. Minor QTL for HM (HM2.1^{BR}) and SW (S2.1^{BR}) colocated with this QTL. Additional minor-effect QTL for yield (SY5.1^{BR} and SY10.1^{BR}) were found on Pv05 (R^2 = 9.2) in NS and on Pv10 (R^2 = 9.1) in DS treatments, respectively. In addition to Pv01 and Pv02, QTL for HM (HM5.1^{BR} and HM8.1^{BR}) were observed on Pv05 (R^2 = 8.2 and 10.3) and Pv08 (R^2 = 12.1 and 16.4) under DS and NS treatments, respectively. A second QTL for DSF2.2^{BR} was observed on Pv02. A major QTL for SW (SW8.1^{BR}) was found on Pv08 for single and combined environments (R^2 = 9.2–33.0).

Phenotypic correlations (Table 6) support colocation of QTL for yield, DF, HM, DSF, and SW on chromosome Pv01 near SNP50809 (47.7 Mb) and QTL for yield, HM, and SW on Pv02 near SNP40055 (11.8 Mb). One mean for DF was used in the correlation analysis as there was no significant difference between DS and NS treatments for this trait. Correlations were observed between DF and yield under MS and NS, 60 and 32% ($p > 0.001$), respectively. The positive correlation between later DF and HM with increasing yield under MS suggests that early maturing

Table 5. Chromosome location and significance for seed yield (SY), days to flowering (DF), days to harvest maturity (HM), seed weight (SW), and days to seed fill (DSF) measured in the 'Buster'/'Roza' (BR) recombinant inbred line population across three locations (Prosser, WA [P]; Othello, WA [WA]; and Mitchell, NE [NE]), three treatments (multiple stress [MS], drought stress [DS], and nonstress [NS]), and two combined environments (Prosser [MP] and Washington and Nebraska [MWN]).

Quantitative trait loci	Environment	Chromosome	Location (Mb)	Closest marker	LOD†	LOD TH	R^2	Add‡
SY1.1^{BR}	MP_MS	1	47.7	SNP50809††	13.9	3.1	36.8	–457.1
	P_2006	1			9.9	3.5	27.8	–466
	P_2007	1			9.8	3.3	27.6	–327.4
	P_2008_MS	1			11.8	3.5	32.2	–217.8
	MWN_NS	1			2.4§	3.4	7.7	–35.3
	NE_2012¶	1			2.6#	3.4	8.3	–50.7
	WA_2011_NS	1			4.1	3.3	12.5	–30.5
SY2.1^{BR}	MP_MS	2	11.8	SNP40055	6.5	3.3	19.3	–312.1
	P_2006	2			7.8	3.2	22.7	–415.8
	P_2007	2			5.6	3.4	16.7	–240.2
	MWN_DS	2			5.3	4	16	–42.2
	NE_2011_DS	2			12.2	3.5	33	–85.4
SY5.1^{BR}	NE_2011_NS	5	38.7	SNP45307	3	3	9.2	–51
SY10.1^{BR}	NE_2011_DS	10	39.9	SNP46337	2.9	2.7	9.1	45.6
DF1.1^{BR}	MWN¶	1	3.3	SNP49655	7.4	3.2	21.5	0.7
	WA_2011¶	1			5.1	3.1	15.3	0.8
	WA_2012¶	1			5.1	3.2	15.5	1.2
	NE_2011¶	1			5.1	4.1	15.5	0.5
	NE_2012¶	1			4.2	3.1	13	0.3
DF1.2^{BR}	MWN¶	1	47.7	SNP50809	24.5	3.2	55.3	–1.5
	WA_2011¶	1			20.3	3.1	48.7	–1.7
	WA_2012¶	1			23.3	3.2	53.6	–3
	NE_2011¶	1			12.9	4.1	34.7	–0.8
	NE_2012¶	1			9.7	3.1	27.3	–0.4
HM1.1^{BR}	WA_2011_DS	1			3.8§	3.1	11.8	–0.2
	NE_2011_NS	1			5.3§	3.3	16	–0.3
	NE_2012_DS	1			3.8§	3.2	11.8	–0.002
HM2.1^{BR}	WA_2011_NS	2	11.8	SNP40055	3	3	9.3	0.1
	NE_2011_DS	2			5.6	3.2	16.8	0.4
HM5.1^{BR}	MWN_DS	5	30.3	SNP49223	2.6	3.2	8.2	–0.04
	MWN_NS	5			3.3	3.2	10.3	0.04
HM8.1^{BR}	WA_2012_NS	8	1.5	SNP47114	5.5	3.3	16.4	–0.6
	WA_2012_DS	8			3.9	2.8	12.1	0.5
SW1.1^{BR}	WA_2011_DS	1	3.3	SNP49655	4	3.1	12.2	0.3
SW1.2^{BR}	WA_2011_DS	1	47.7	SNP50809	6.8	3.1	20.1	–0.4
SW2.1^{BR}	NE_2012¶	2	11.8	SNP40055	3.5	3.1	10.8	0.8
SW8.1^{BR}	WA_2011_NS	8	58.6	SNP46750	3.0#	3.0	9.2	0.3
	WA_2012_NS	8			2.8#	2.3	8.6	0.1
	NE_2012¶	8			12.2	3.0	33.0	1.4
SW8.2^{BR}	MNW	8	59.3	SNP47387	3.9	3.1	12.0	0.1
	NE_2011_NS	8			4.5	2.9	13.7	0.2
DSF1.1^{BR}	WA_2011_DS	1	47.7	SNP50809	4.3	3.6	13.3	–0.27
	NE_2011_NS	1			4.3	3.1	13.2	–0.39
DSF2.1^{BR}	WA_2011_NS	2	37.9	SNP47866	2.7#	2.5	8.6	0.17
DSF2.2^{BR}	NE_2011_DS	2	26.8	SNP46834	3.2	6.4	19.0	0.66

† LOD, logarithm of odds; LOD TH, LOD thresholds calculated by performing 1000 permutations at $P = 0.01$.

‡ Values represent effect from 'Buster' allele.

§ Quantitative trait loci (QTL) is significant with SNP49655 (QTL associated with phenology traits) as an additional cofactor.

¶ Best linear unbiased predictors for genotype only were used for detecting QTL, as there was no significant difference between drought stress and nonstress.

QTL reported is significant at $P = 0.05$ and only reported if additional QTL are reported at the same location at $P = 0.01$.

†† Note that SNP names are truncated from ss7156_____.

Table 6. Pearson correlation coefficients (*r*) of seed yield (SY), 100-seed weight (SW), days to flowering (DF), days to harvest maturity (HM), and days to seed fill (DSF) under multiple stress (MS; SY only) at Prosser, WA, and drought stress (DS), and nonstress (NS) treatments at Othello, WA, and Mitchell, NE.

	SY			SW		DF†	HM		DSF	
Trait	MS	DS	NS	DS	NS		DS	NS	DS	NS
SY MS	–									
SY DS	0.46***	–								
SY NS	0.17*	−0.60***	–							
SW DS	0.00	0.00	0.12	–						
SW NS	−0.09	−0.02	−0.12	−0.91***	–					
DF	0.60***	0.08	0.40***	0.18*	−0.18*	–				
HM DS	−0.11	−0.40***	0.33***	0.22**	−0.22**	0.30***	–			
HM NS	0.32***	0.35***	−0.05	−0.15	0.19**	0.06	−0.87***	–		
DSF DS	0.01	−0.38***	0.49***	0.16	−0.07	0.33***	0.68***	−0.29***	–	
DSF NS	0.14	0.08	0.00	0.23**	−0.29***	0.16	0.26**	−0.24**	0.12	–

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

† Best linear unbiased predictor analysis showed no treatment effect for DF; therefore, one mean was used in the correlation analysis.

genotypes were not able to escape the intermittent drought stress as they seemed to under terminal drought (discussed below). Significant negative correlations indicate the importance for shorter DSF for increased SY for this population under DS. Yield under MS showed a stronger correlation with yield under DS vs. NS. These correlations suggest that drought tolerance is an important component of the contrasting response to stress between Buster and Roza. Two other highly significant negative correlations occurred for SW between treatments and HM between treatments. These warrant further discussion below.

DISCUSSION

Environmental conditions (low rainfall amounts and warm temperatures) and the combination of soil compaction, low fertility, root rot, and imposed intermittent drought stress enabled MS testing for 3 yr at Prosser, WA. Low mean yield for the RIL populations (1526–2613 kg ha^{-1}) and vast differential response in yield between the parents (Roza yielded 58% more than Buster) support that a high level of multiple stress was achieved. Year 2008 provided the only direct comparison between NS and MS treatments. Although the 2008 trial exhibited the least stress, as indicated by higher mean scores for the parents and RIL population, there was still a large difference in performance between the parents.

Low rainfall amounts and warm temperatures enabled us to impose terminal drought stress in 2011 and 2012 at Othello, WA, and Mitchell, NE, by ceasing irrigation after flowering. Although, less severe drought stress occurred in 2012 for both locations, a broad range for PR in response to drought stress was observed among RILs for both years (2011: WA = 18–83%, NE = 8–85%; 2012: WA = 0–60%, NE = 6–80%).

In this study, we identified stable QTL across multiple levels of stress and environments using BLUPs. Data were also analyzed using least-square means, and similar results were obtained; however, due to the consequential overestimation that can occur in detecting QTL in relatively small mapping populations (Kuchel et al., 2007; Bernardo, 2002), the more conservative BLUP was used in this study. There were two main differences in using BLUPs vs. least-square means: i) a single mean was used for mapping when neither a treatment effect nor genotype-by-treatment interaction occurred and ii) fewer minor QTL were detected.

Consistant QTL for SY were detected on Pv01 (SY1.1) and Pv02 (SY2.1) under MS (Fig. 1). SY1.1 and SY2.1 are considered major because each of them were detected in multiple environments. Together, SY1.1 and SY2.1 had an additive effect, explaining 56% of the phenotypic variance for combined yield under MS and 16% under DS. SY1.1 and SY2.1 have larger effect in comparison to the QTL identified for yield in other studies (Mukeshimana et al., 2014 [R^2 = 8.3–20.2%]; Asfaw et al., 2012 [R^2 = 9–14%]; Blair et al., 2012 [R^2 = 11–24%]). Of known QTL for SY found under drought conditions (Asfaw et al., 2012; Blair et al., 2012; Mukeshimana et al., 2014), none were located on Pv02. Asfaw et al. (2012) found a QTL for SY under NS on Pv01 (R^2 = 11%) near SSR marker BM200 (30.8 Mb).

Because the purgatory plot exerts multiple stresses on yield performance it is difficult to attribute the SY1.1 and SY2.1 QTL as a response to any one stress. The expression of SY1.1 and SY2.1 in the terminal drought trials help to decode which stresses the QTL may be expressed against. Independently, SY1.1 was only detected in the NS treatments (2011 Washington, 2012 Nebraska, and combined location-years). Roza contributes the SY1.1 allele for multiple stress tolerance in this case and the same allele conditions a minor influence on yield under NS and interacts with SY2.1 under DS.

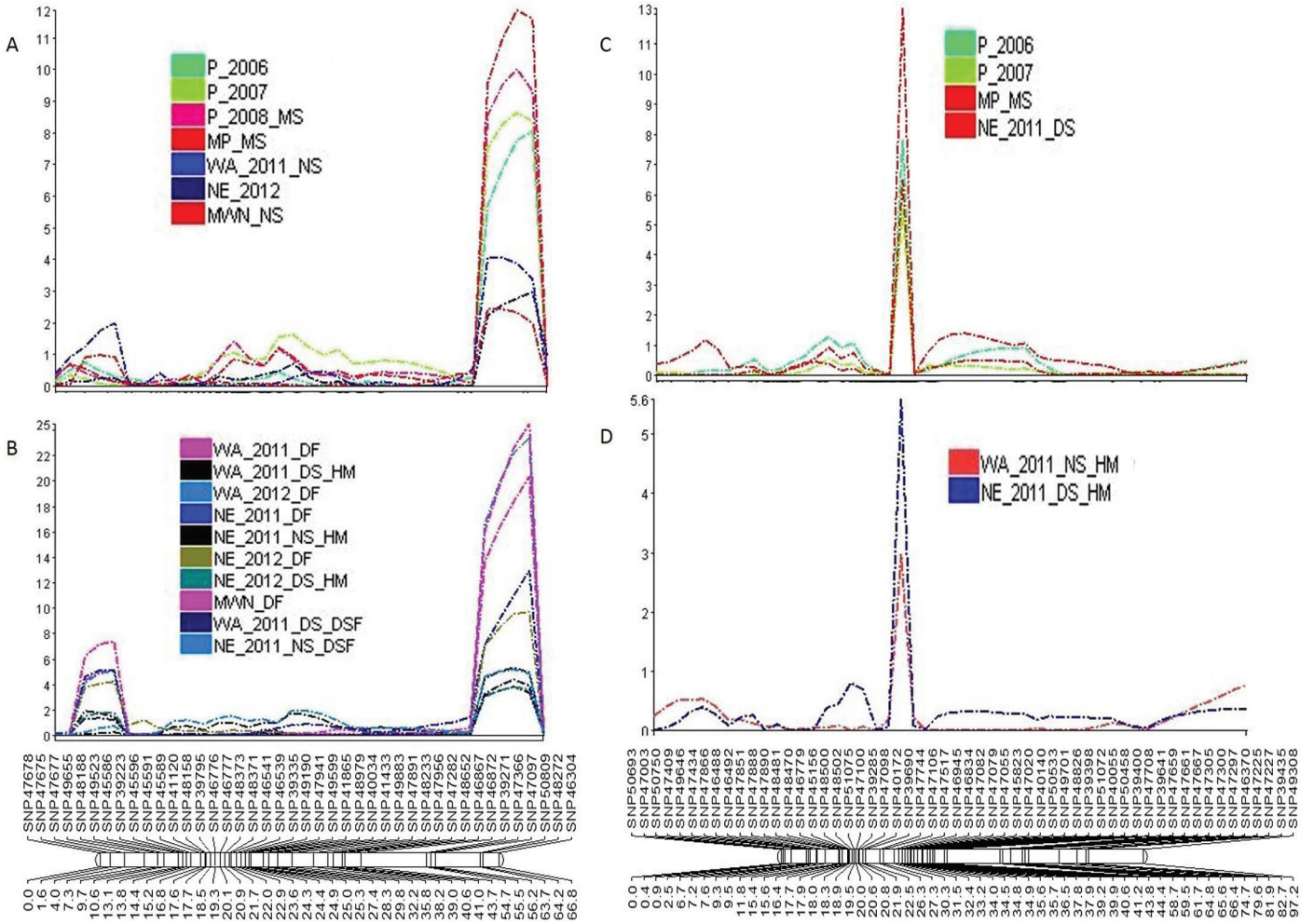

Figure 1. Composite interval mapping logarithm of odds (LOD) displaying molecular markers (single nucleotide polymorphism) and distance (cM) linked with drought-related quantitative trait loci (QTL) in the 'Buster'/'Roza' recombinant inbred line mapping population of common bean. Chromosomes (Pv01 and Pv02) with major-effect QTL are shown across locations: P, Prosser, WA; WA, Othello, WA; NE, Mitchell, NE; MWN, Othello, WA, and Mitchell, NE; MP_MS, Prosser combined years under multiple stress; DS, drought stress; NS, nonstress. (A) Yield QTL on Pv01; (B) Phenological traits on Pv01; (C) Yield QTL on Pv02; and (D) Phenological traits on Pv02. Note SNP names are truncated from ss7156_____.

Shorter DSF duration under DS was associated with increased yield under DS treatment ($r = -0.38$; $p < 0.001$) while longer DSF under DS was positively correlated with yield under NS ($r = 0.49$; $p < 0.001$). There was no significant correlation between DSF under NS and yield under NS (Table 6). Separating RILs into drought-tolerant and drought-susceptible showed that as a group, the tolerant lines were better able to adapt to the drought stress by decreasing DSF by 2 d compared with the susceptible group. These correlations support that RILs with higher yields under stress were more effective and efficient (shorter DSF) in partitioning yield from vegetative to reproductive growth.

The colocation of QTL for DF, HM, and DSF with SY1.1 (Fig. 1; Table 5) suggests phenology contributes to the effect of this yield QTL. Generally, later maturity is associated with higher yield in most environments given that the late maturity is not associated with lack of adaptation (Kelly et al., 1998). Later maturity (increasing HM) was not correlated with yield under NS in the BR RIL population, indicating that later maturity does not influence yield under stress, per se, but is manifested as a means of adaptation to the MS conditions in the purgatory plot. Moreover, under MS, delayed flowering might enable plants to spend more energy on root growth and development to better withstand intermittent drought and the other stresses imposed. The same mechanism was not effective for terminal drought as there was no correlation between DF and yield under DS. In fact, later maturity was associated ($r = -0.40$; $p < 0.001$) with lower yield and represented a lack of adaptation under terminal drought stress. This late maturity, indicating lack of adaptation in response to terminal drought, is further supported by the complete inverse negative relationship ($r = -0.87$; $p < 0.001$) for HM between DS and NS. Early maturing lines, which could avoid terminal drought, were the same lines that were later maturing without drought. This suggests developmental plasticity as an

escape to terminal drought stress. Yield between DS and NS is similarly negatively correlated ($r = -0.60$; $p < 0.001$). This result indicates that selection for yield under drought will not improve yield under nonstress or vice versa. Therefore, at least for the BR RIL population, individual selection for high yield in both environments using GM as a selection index would be a necessary strategy to improve yield under stress and nonstress conditions.

Several other studies have reported plasticity as a drought response mechanism in dry bean (Vallejo and Kelly, 1998; Terán and Singh, 2002; Rosales-Serna et al., 2004; Urrea et al., 2009; Mukeshimana et al., 2014), and QTL conditioning phenology have also been reported on Pv01 (Koinange et al., 1996; Kwak et al., 2008; Mukeshimana et al., 2014). Wallace et al. (1993a,b) concluded that a photoperiod gene interacts with day length and temperature (Padda and Munger, 1969), thereby controlling shoot biomass, harvest index, and the number of days to maturity. It is likely that the previous QTL conditioning phenology on Pv01 is the same photoperiod gene described by Wallace et al. (1993a) that has major influence on partitioning between reproductive and vegetative growth. Gu et al. (1994) reported an additional photoperiod gene, *Hr*, which interacts with *Ppd* causing differential expression of partitioning rates dependent on air temperature. Their marker study in 1998 (Gu et al., 1998) estimated the two genes to be approximately 40 cM apart. With 57 cM between DF1.1 (SNP 49655; 3.3 Mb) and DF1.2 and associated phenology traits DSF1.1 and HM1.1 (SNP 50809; 47.7 Mb), it is possible that DF1.1 and DF1.2 QTL reported herein on Pv01 are the same *Hr* and *Ppd* genes reported by Gu et al. (1994). We observed that DF1.2 is not significant without the presence of DF1.1 and that in some instances the presence of DF1.1, though not significant, increased the significance of DF1.2. That the photoperiod gene *Hr* is influenced by temperature could be a potential reason why DF1.1 was not detected in all environments. In addition, DF1.2 (47.7 Mb) physically mapped distally near the potential candidate gene for the *fin* locus *PvTFL1y* (45 Mb), affecting determinacy growth habit. Similarly, *Ppd* genetically mapped about 5 cM distally from *fin* (Kwak et al., 2008).

It is unsurprising that phenology QTL are influenced by timing and intensity of water stress endured by the plant thereby making it difficult to discern adaptive vs. constitutive QTLs. However, recent development of an annotated reference genome sequence (www.phytozome.net) for common bean (Schmutz et al., 2014) has enabled physical mapping of targeted traits as well as a more accurate mapping of genes underpinning targeted traits, thus, making the search for potential adaptive QTL more feasible. Using the BLAST option in Phytozome (http://www.phytozome.net), transcription factors zinc finger (Phvul.001G213800) and WRKY DNA-binding domain (Phvul.001G213600) associated with drought stress in dry bean (Recchia et al., 2013) were found near SY1.2 (47.7 Mb). Also located on Pv01, but near DF1.1 (3.3 Mb), were candidate genes for abscissic acid (Phvul.001G034300) and histone deacetylase (Phvul.001G034500). The abscissic acid hormone response has been associated with drought stress (Blum 2011) and histone deacetylases have been reported as a key component in flowering and senescence as well as environmental stresses in *Arabidopsis thaliana* L. (Hollender and Liu, 2008). In addition, Müller et al. (2014) reported differentially expressed genes during flowering and grain filling between drought-tolerant BAT 477 and drought-susceptible Pérola, one of which was a Zn finger protein located on Pv01 at 49 Mb (GI:356539989). Recchia et al. (2013) also reported a Zn finger protein at 49 Mb and a WRKY protein at 48 Mb. Further studies are necessary to determine whether the SY1.1 QTL is strictly in concordance with the *Ppd* photoperiod gene or controlled by one or more of the putative candidate genes for drought stress mentioned above.

Table 7. Quantitative trait loci summary of additional seed yield (SY) parameters: geometric mean (GM) and percentage reduction in yield (PR) from combined location-years (Othello, WA and Mitchell, NE [MWN]).

Environment	Trait	Linkage group	Closest marker	LOD†	LOD TH	R^2	Add‡
MWN_GM	SY	1	50809	6.3	3.5	18.7	–220.3
MWN_GM	SY	2	40055	2.5	2.4	7.8	–131.4
MWN_PR	SY	2	40055	5.2	3.7	15.6	3.4

† LOD, Log of odds; LOD TH, LOD thresholds calculated by performing 1000 permutations at $P = 0.01$.

‡ Positive values represent effect from 'Buster' and negative values represent effect from 'Roza'.

The SY2.1 yield QTL on Pv02 may be in response to the imposed intermittent drought stress component of the multiple stresses in the purgatory plot because it was detected in the terminal drought treatments. While QTL for geometric mean for yield mapped to SY1.1 and SY2.1, PR in SY between DS and NS treatments mapped solely to SY2.1, providing further support for the response of this QTL specifically to DS (Table 7). Furthermore, SY2.1 was a significant component for yield under DS and MS but not NS in the multiple regression analysis.

Seed weight (SW2.1) and HM2.1 colocated with SY2.1 under NS in Washington and DS in Nebraska in 2011 (Fig. 1; Table 5). Interestingly, SW was highly negatively correlated ($r = -0.91$) between DS and NS across location-years. The ranges for combined mean SW in either treatment was relatively narrow, 35 to 36.1 g 100 seeds^{-1} for drought stress and 37.3 to 38.7 g 100 seeds^{-1} for nonstress. Seed weight for all RILs was reduced under the DS treatment; however, the larger seeded lines had a greater reduction in SW than the slightly smaller seeded lines. The decrease in SW between DS and NS treatments ranged from 1.2 to 3.7

g 100 seeds^{-1} with the greater reductions associated with the slightly larger seeded lines. The more drought-tolerant parent Roza is smaller seeded (33 g 100 seeds^{-1}) than Buster (43 g 100 seeds^{-1}) under NS conditions, which may have influenced this highly negatively correlated response between the DS and NS treatments.

Two putative drought-related candidate genes are in close proximity to the SY2.1 QTL identified on Pv02: calcineurin-like phosphoesterase (Phvul.002G078800) and Myb-like DNA binding domain (Phvul.002G078600). The Myb transcription factor family has already been reviewed as an important component in the regulation of abiotic stress (Ambawat et al., 2013) and has been expressed in soybean [*Glycine max* (L.) Merr.] (Su et al., 2014) and dry bean (Recchia et al., 2013) under drought stress.

For both Pv01 (DF1.2, HM1.1, and DSF1.1) and Pv02 (DF2.1 and HM2.1) associated QTL conditioning phenology traits, the allele from Buster is associated with low yield. For Pv01 QTL, the Buster allele conditioning earlier DF and HM contributed to the lower yield in the MS trials. For the HM2.1, the Buster allele contributed to later maturity under terminal drought, which was correlated with lower yield. The Buster allele for HM5.1 and HM8.1 had contrasting effects in NS and DS environments.

SUMMARY

The QTL for yield under MS identified in this study exhibited differential expression in the terminal drought trials with SY1.1 expressed under NS and SY2.1 expressed in the DS treatment. Phenological traits DF, HM, and DSF colocated with SY1.1 and interacted with another QTL on Pv01, which conditioned DF. These two QTL regions (3.3 and 47.7 Mb) on Pv01 may represent the *Hr* and *Ppd* genes. Phenology was associated with the SY2.1 QTL. Clearly, plasticity in phenological response affected yield under MS, DS, and NS. These findings, in addition to the significant negative correlation for yield between DS and NS treatments, contradict selecting for yield potential under drought stress transferring to high yield under nonstress, at least in this population. Selection for yield in target environments is still the best way for identifying drought-tolerant lines. Although SY1.1 and SY2.1 were predominant in MS environments, QTL SY2.1 was also detected under DS, which makes it potentially useful in breeding for drought tolerance as well. Moreover, the additive effect of SY1.1 and SY2.1 for yield under DS may represent an important contribution to breeding for drought tolerance. Validation of the SY1.1 and SY2.1 QTL in additional populations is needed to verify their importance for marker-assisted breeding.

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