Deciphering Genomic Regions Associated with Waterlogging and Drought Tolerance Traits in Tropical Maize using Multiple, Connected Populations

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Introduction

Changes in the global climate are now a reality; these changes have become more complex and unpredictable, effecting agriculture in general and maize production in particular, globally (WMO, 2007, 2011; Zaidi and Singh, 2005). The erratic distribution pattern of monsoon rains results in unpredictable occurrence of drought and waterlogging at high intensity and scale. This is one of the most serious constraints for maize production, particularly for South and Southeast Asia, where 80 percent of the maize cultivated area is still rainfed (IFAD, 2002; Osman et al., 2013; Zaidi et al., 2002; Zaidi and Singh, 2005). The unpredictability and frequent occurrences of waterlogging and drought within a maize cropping season in this region, implies the need for germplasm that has reasonable tolerance to both these major abiotic stresses.

Waterlogging at the vegetative stage (V5) and drought at flowering, are reported as the most critical stages to maize crop (Messmer et al., 2011; Zaidi and Singh, 2005). Breeding for drought and waterlogging tolerance is complicated due to their polygenic nature and the large influence of environment on the trait phenotypes (Bernardo and Yu, 2007; Bernardo et al., 2006; Collins, 2008; Rahman et al., 2011; Zou, et al., 2010). Conventional methods of breeding though successful (Borlaug and Dowswell, 2005; Campos et al., 2004; Duvick and Scott, 2005; Rebetzke et al., 2002; Reynolds and Tuberosa, 2008; Ribaut et al., 2004), rely mainly on phenotypes being evaluated in several environments; and selection and recombination based solely on the resulting data and pedigree information, if available. However, the complex nature of these traits, along with the need for repeated screening of large breeding materials, is resource- and labor- intensive. Methodologies that could aid in efficient selections circumventing these necessities would greatly assist breeders in achieving larger genetic gains.

With rapid advances in molecular marker technology in maize, it is now feasible and cost-effective to apply molecular markers efficiently, in marker-assisted breeding programs, for such complex traits as waterlogging and drought (Zobel, Wright et al., 1988). Drought stress is one of the most-studied traits across crops. In maize, literature is abundant on genomic regions signifying drought tolerance, such as regions on chromosome 1 and 10 (Ribaut et al., 1997) and 7 (Almeida et al., 2013) contributing to adaptive QTL for grain yield under drought stress. Additionally, important genomic regions of several secondary traits associated with drought tolerance, such as Anthesis-silking interval, or ASI (chromosome 3), senescence (chromosome 1, 3, 6, 8 and 10), root traits (chromosome 10) have also been identified (Bolaños and Edmeades, 1996; Coque et al., 2008; Gallais and Hirel, 2004; Almeida, et al., 2013; Messmer et al., 2009; 2011; Ribaut et al., 1997; Zhang et al., 2008). Several genomic regions have been independently identified for waterlogging tolerance traits such as on chromosomes 1, 4, 5, 6, 8 and 9 (Mano et al., 2005; 2006; 2009; 2008; Osman et al., 2013; Sérgio Tadeu Sibov et al., 2003; Xue et al., 2013; Zhang et al., 2014). Zou et al. (2010) identified 296 unigenes of which 63 co-located with previously identified QTL contributing to late waterlogging tolerance. These genes were found to be involved in complex bio-chemical pathways such as signal transduction and protein degradation, etc. Furthermore, while all these studies have independently identified genomic regions for these traits, no study reports genomic regions associated commonly with both waterlogging and drought tolerance. Given all of the genomic information available, marker-assisted selection (MAS) has had little success in the public domain with minor contribution to development and release of successful cultivars (Bernardo, 2008). Collins et al. (2008) suggests this to be due to the fact that during MAS strategy formulation interactions between multiple stresses are seldom considered and each stress are considered independently, while in nature, crop-cycles encounter multiple stresses. In addition, QTL effects are not universal across population and interaction of QTL × population would act as a major hindrance to success of MAS (Malosetti et al., 2008).

With this background, the study was conceptualized to identify an ensemble of stable genomic regions contributing to drought and/or waterlogging tolerance, across a set of 8 tropical maize mapping populations,

representing the two major heterotic groups (comprised of four populations each).

Materials and methods

A total of eight populations constituting 790 $F_{2:3}$ families were developed for this study. These families were aligned to two heterotic groups (A and B), with each group consisting of a common drought- tolerant female donor parent and several waterlogging-tolerant male parents, in the same heterotic group. The schematic representation of the cross development is presented in Figure 1 and the details of crosses and families constituted are presented in Table 1.

The $F_{2:3}$ families, along with their parental lines, were evaluated for grain yield and anthesis-silking interval (ASI). Experiments were laid out as an alpha lattice, with two replication, single-row plots at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), farm in Hyderabad, India during 2012-2014, following standard agronomic practices to maintain a good crop stand. These trials were subjected to three water management schemes as described in earlier reports (Zaidi, 2000, 2012; Zaidi and Singh, 2005), by altering the irrigation pattern: 1) Optimal or well–watered; 2) Flowering stage drought; and 3) Vegetative stage waterlogging.

1) Optimal management: The $F_{2:3}$ families along with the parental lines were evaluated for their performance under well-watered condition during the *Kharif* season (rainy season) of 2013, under optimal water levels. The experiments were monitored on regular intervals and flood irrigations provided at 8-11 days interval, except when moisture in the fields were sufficient due to rainfall.

2) Flowering stage drought management: The experimental materials were planted during the *Rabi* 2013 and *Rabi* 2014 (post-rainy season) for flowering-stage, drought evaluations. Standard irrigation practices were followed until V5-V6 stage of the crop plant; thereafter, irrigations were stopped for a period of over one month. During this drought period, soil moisture was monitored weekly, using moisture profile probes placed at every block in the field. Irrigations were resumed and continued as per schedule, when the soil moisture at 40-60 cm soil depth (maximum active root zone) reached permanent wilting point.

3) Vegetative stage waterlogging management: Experimental materials were evaluated for vegetative stage waterlogging during *Kharif* season of 2013. Waterlogging treatment was applied through flooding of the field with water at the knee-high stage (V5-V6 growth stage) continuously for seven days at a depth of 10±0.5cm. The experimental materials were kept at the same height of immersion by supplying water at a rate that exceeded infiltration and evaporation. After completion of the stress treatment, the field was completely drained-out and irrigation resumed as per schedule.

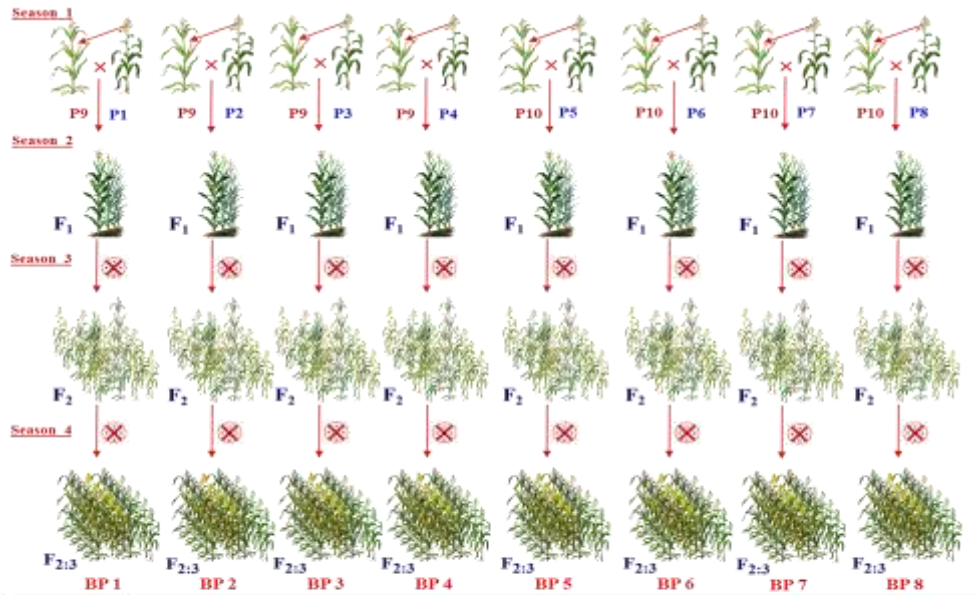

Figure 1. Schematic representation of 790 $F_{2:3}$ families from eight biparental crosses

Table 1. Crosses involved in development of 790 F2:3 families

Population	Crosses (Drought tolerant female / waterlogging tolerant male)	F2:3 families
BP1	DTPYC9-F46-3-9-1-2-2-1-3-B/Saracura-11-3-2-2-1-B	121
BP2	DTPYC9-F46-3-9-1-2-2-1-3-B/WL-18-1-2-2-3-1-B	117
BP3	DTPYC9-F46-3-9-1-2-2-1-3-B/(CML165xCL-02839)-B-22-1-1-BB-1-B	82
BP4	DTPYC9-F46-3-9-1-2-2-1-3-B/WLS-F211-2-2-2-B-2-B	103
BP5	CA03130-BB-3-B-1-B/(DT/LN/EM-46-3-1xCML311-2-1-3)-B-F303-1-1-1-B	103
BP6	CA03130-BB-3-B-1-B/(DT/LN/EM-46-3-1xCML311-2-1-3)-B-F239-1-1-1-B	105
BP7	CA03130-BB-3-B-1-B/WLS-F310-3-2-2-B-1-B	61
BP8	CA03130-BB-3-B-1-B/(DT/LN/EM-46-3-1xCML311-2-1-3)-B-F12-1-1-1-1-B	98
	Total	790

The best linear unbiased estimates were obtained for all families using R software (R Development Core Team, 2008). Entries were treated as fixed effects and blocks and replications as random effects for individual environment analysis. As the experimental material were evaluated for drought stress tolerance for two seasons, Genotype × drought management were considered as random effect to obtain an across environment unbiased estimates.

Genotyping

Genomic DNA was extracted from young leaves, collected in a bulk, from 10 plants per $F_{2:3}$ family, according to CIMMYT's laboratory protocols (CIMMYT, 2001). The parental lines were screened for polymorphism using a set of 1250 SNP markers, for which KASP assays (Semagn et al., 2013) were designed at LGC genomics in London, UK. These 1250 SNPs were a subset of 1536 SNPs (Yan et al. 2010). A total of 1186 polymorphic SNPs were identified across the parental lines, which were used to screen the $F_{2:3}$ families (Table 2). A linkage map was constructed using QTL IciMapping ver. 3.2 software (*http://www.isbreeding.net*). Initially, the linkage map was developed for each population separately for subsequent QTL analysis. The Haldane mapping function was used to convert the recombination frequency to genetic distances in centimorgans (cM). As no polymorphic marker could be identified across parent 10 and parent 8, the eighth biparental population was dropped from this study. The details of the linkage map constructed and the average inter marker distances are presented in Table 2.

Table 2. Marker distribution details across eight $F_{2:3}$ families

Population	*Cross	No. of F2:3 families	No. of polymorphic Markers	Linkage distance (cM)	Average inter marker distance
BP1	P9 × P1	121	107	781.77	7.31
BP2	P9 × P2	117	140	726.58	5.19
BP3	P9 × P3	82	75	561.92	7.49
BP4	P9 × P4	103	159	880.57	5.54
BP5	P10 × P5	103	63	385.73	6.12
BP6	P10 × P6	105	209	1142.42	5.47
BP7	P10 × P7	61	118	1039.81	8.81
BP8	P10 × P8	98	0	0.00	0.00

*P9 and P10 drought tolerant female lines and P1 to P8 waterlogging tolerant male lines

A composite interval mapping approach (Jansen and Stam, 1994) was followed to detect QTL using the best, linear, unbiased, estimates obtained for observed trait of each population under three different managements using QTL cartographer v2.5 (Basten et al., 2010). An sdditive + dominant model was used to detect the QTL. A QTL was considered to be present if the association crossed a LOD threshold of 2.5. Two QTL detected were declared as congruent if they were within 20cM distance and/or were detected in at least two or more populations at similar locations (Melchinger et al., 1998). The gene action of each QTL were classified as additive, partial dominant, dominant and over dominant based on the level of dominance based on the criterion by (Stuber et al., 1987a; Stuber et al., 1987b). Each of the QTL identified were designated based on the trait, management, population and chromosomal position; for instance a QTL for grain yield under optimal management determined in BP7 on chromosome 1 was named GY_D_BP7_1.1 while a second QTL identified in the same region for drought on a different population was designated as GY_D_BP4_1.2. The two trait designations used for this nomenclature were GY (grain yield) and ASI (anthesis-silking interval) while the three management schemes were designated as O (Optimal), D (Drought) and W (waterlogging); and the seven populations were designated as BP1 to BP7.

Results

Phenotypic characterization

The parental lines of all the eight populations differed substantially for most tolerance traits. As expected, the female parental lines were superior under drought management, as compared to the male lines that were superior under managed waterlogging stress (Table 3). Substantial variation was observed among the $F_{2:3}$ families along with transgressive segregations exceeding the parental trait values (data not shown), suggesting dispersion of favorable and unfavorable alleles among the parental lines (Table 3).

G×E interaction across drought management for the traits observed were not substantial. Heritability estimates across population and management were moderate to high, except for grain yield in BP3 under drought stress. A comparison of three managements revealed a penalty of 20-50 percent for grain yield, under drought and 30-80 percent under waterlogging stress, across the population as compared to optimal management. Similar reductions were also observed among the parental lines under the two stress managements. In general, the penalty under waterlogging seemed more severe than under drought stress (Figure 2) across populations. ASI widened under drought and waterlogging stress managements across populations and parental lines suggesting a similar influence of drought and waterlogging on the reproductive mechanism.

Table 3. Descriptive statistics for agronomic and recorded on eight (DT×WL) $F_{2:3}$ populations

Population	Statistic	GY			ASI		
		D	O	W	D	O	W
BP1	$F_{2:3}$ (Mean)	1.37±0.15	1.87±0.20	0.47±0.10	1.6±0.5	0.4±0.2	2.2±1.0
	Range	0.34-2.28	0.85-3.77	0.0-1.89	0.0-4.2	0.0-7.9	0.0-16.0
	σ^2_g	0.09	0.37	0.11	0.1	0.4	0.1
	$\sigma^2_{g\times env}$	0.12			0.4		
	h^2	0.47	0.76	0.73	0.2	0.3	0.0
	$\hat{r}_g$ with optimal	0.69***		0.6***	0.38***		0.19*
BP2	$F_{2:3}$ (Mean)	1.13±0.13	1.81±0.20	0.37±0.20	2.7±0.6	1.7±0.3	2.2±0.7
	Range	0.35-1.97	0.85-3.18	0.0-0.95	0.0-7.3	0.0-11.5	0.0-15.0
	σ^2_g	0.10	0.40	0.22	0.8	1.1	0.0
	$\sigma^2_{g\times env}$	0.07			1.1		
	h^2	0.55	0.80	0.75	0.5	0.3	0.0
	$\hat{r}_g$ with optimal	0.53***		0.32**	0.36***		0.0
BP3	$F_{2:3}$ (Mean)	1.12±0.16	1.63±0.20	1.04±0.30	0.8±0.5	0.2±0.4	2.4±0.7
	Range	0.41-2.09	0.43-3.01	0.00-3.35	0.0-9.0	0.0-8.5	0.0-14.1
	σ^2_g	0.02	0.61	0.79	0.9	1.0	1.0
	$\sigma^2_{g\times env}$	0.01			0.9		
	h^2	0.22	0.85	0.86	0.5	0.3	0.3
	$\hat{r}_g$ with optimal	0.65***		0.51***	0.40***		0.50***
BP4	$F_{2:3}$ (Mean)	1.29±0.20	2.51±0.20	0.74±0.30	2.4±0.5	0.7±0.3	4.2±0.7
	Range	0.55-2.03	1.00-3.94	0.00-1.77	0.5-4.5	0.0-6.8	0.1-0.0
	σ^2_g	0.03	0.39	0.52	0.0	0.2	1.5
	$\sigma^2_{g\times env}$	0.12			1.0		
	h^2	0.21	0.75	0.78	0.0	0.2	0.3
	$\hat{r}_g$ with optimal	0.62***		0.55***	0.44***		0.1

BP5	$F_{2:3}$ (Mean)	1.28±0.15	1.64±0.20	0.65±0.30	3.0±0.4	1.7±0.6	2.6±0.5
	Range	0.53-2.31	0.48-2.97	0.00-1.98	1.1-5.6	0.0-7.0	0.0-9.4
	σ^2_g	0.09	0.59	0.78	0.0	0.2	0.6
	$\sigma^2_{g\times env}$	0.12			0.4		
	h^2	0.55	0.84	0.86	0.0	0.2	0.3
	$\hat{r}_g$ with optimal	0.47***		0.64***	0.34***		0.1
BP6	$F_{2:3}$ (Mean)	0.91±0.14	1.56±0.20	0.94±0.30	3.9±0.6	2.0±0.7	2.2±0.4
	Range	0.17-1.75	0.09-2.88	0.00-2.27	0.0-10.2	0.0-6.6	0.0-7.0
	σ^2_g	0.15	0.46	0.7	1.8	0.7	0.4
	$\sigma^2_{g\times env}$	0.04			0		
	h^2	0.69	0.85	0.85	0.6	0.4	0.3
	$\hat{r}_g$ with optimal	0.53***		0.68***	0.47***		0.15*
BP7	$F_{2:3}$ (Mean)	0.89±0.18	1.31±0.30	0.82±0.50	3.3±0.6	2.4±1.4	2.6±0.4
	Range	0.34-2.17	0.24-2.7	0.00-2.13	0.9-7.1	0.0-11.5	0.0-6.0
	σ^2_g	0.23	0.27	0.36	0.6	1.3	0.1
	$\sigma^2_{g\times env}$	0.04			0.1		
	h^2	0.66	0.51	0.71	0.5	0.4	0.1
	$\hat{r}_g$ with optimal	0.66***		0.54***	0.26**		0.24**
BP8	$F_{2:3}$ (Mean)	0.74±0.13	1.21±0.20	0.37±0.20	3.7±0.5	1.8±0.7	3.2±0.5
	Range	0.11-1.71	0.07-2.67	0.00-1.71	0.7-10.5	-14.0	0.9-8
	σ^2_g	0.14	0.65	0.46	1.4	1.9	0.6
	$\sigma^2_{g\times env}$	0.10			1.2		
	h^2	0.58	0.89	0.86	0.5	0.8	0.2
	$\hat{r}_g$ with optimal	0.69***		0.75***	0.35***		0.1
	$P1_{(Mean)}$	*0.53±0.17*	*0.97±0.30*	*0.00±0.20*	*3.0±0.8*	*0.9±0.9*	*2.5±0.7*
	$P2_{(Mean)}$	*0.22±0.22*	*0.76±1.20*	*0.42±0.20*	*6.3±2.2*	*4.0±1.0*	*2.5±0.5*
	$P3_{(Mean)}$	*0.94±0.22*	*1.40±0.60*	*0.67±0.30*	*3.3±1.1*	*4.0±0.9*	*1.9±0.4*
	$P4_{(Mean)}$	*0.67±0.21*	*1.37±0.50*	*0.56±0.30*	*3.0±1.0*	*1.4±0.5*	*1.4±0.7*
	$P9_{(Mean)}$	*1.31±0.25*	*1.43±0.20*	*0.29±0.20*	*1.6±0.9*	*0.6±1.0*	*2.8±0.5*
	$P5_{(Mean)}$	*1.14±0.45*	*2.38±0.50*	*0.47±0.50*	*1.6±1.0*	*2.5±2.6*	*2.0±0.4*
	$P6_{(Mean)}$	*0.23±0.21*	*1.28±0.20*	*0.59±0.40*	*6.0±1.3*	*3.4±2.6*	*2.5±0.5*
	$P7_{(Mean)}$	*0.40±0.17*	*0.83±0.30*	*0.69±0.50*	*1.6±1.6*	*1.0±1.4*	*2.2±0.4*
	$P8_{(Mean)}$	*0.17±0.09*	*0.56±0.10*	*0.40±0.30*	*4.3±1.5*	*2.0±2.8*	*1.9±0.4*
	$P10_{(Mean)}$)	*0.91±0.22*	*1.55±0.20*	*0.29±0.10*	*4.0±0.8*	*2.4±2.3*	*2.8±0.7*

GY: Grain yield (t/ha), **ASI**: anthesis-silking interval (days),

h^2: Heritability; **σ^2_g:** Genotypic variance; **σ^2_{gxenv}:** Genotype×environment variance; **$\hat{r}_g$**: genotypic correlation coefficients between Drought (**D)** and optimal management (**O**) and between Waterlogging (**W**) and optimal management (O);

P9 and P 10: DT parent; **P1 to P8** Waterlogging tolerant parent; **BP:** Biparental population

*, **, *** Significance at P = 0.05; 0.001 and 0.001 levels, respectively.

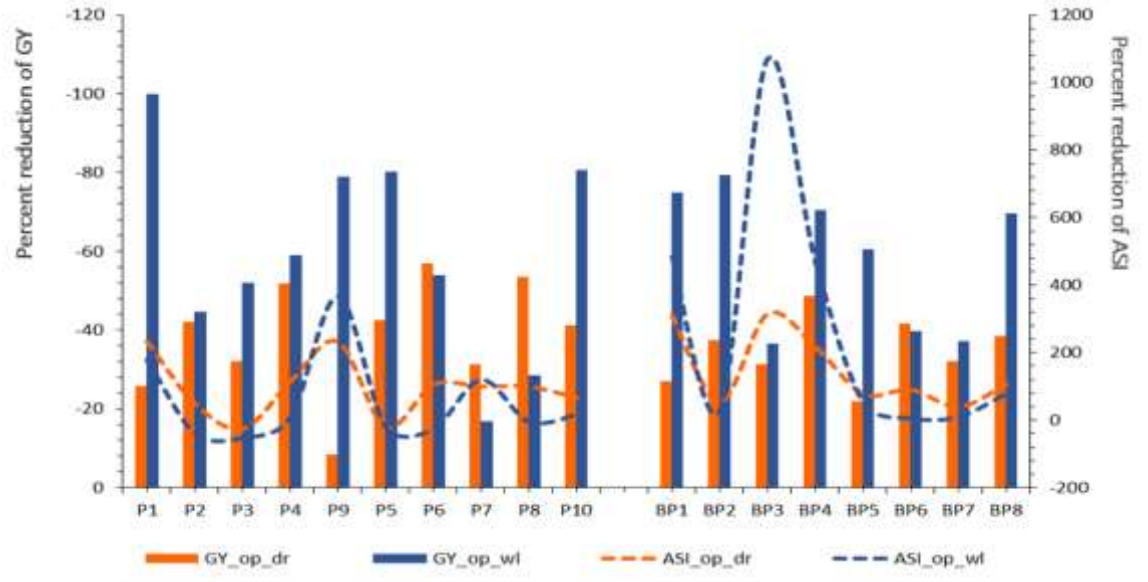

Figure 2. Average percent reduction of grain yield (GY) and increase of anthesis-silking interval (ASI) across drought and optimal (op_dr) and across Waterlogging and optimal (op_wl) managements in eight F2:3 biparental population (BP1 to BP8) and their parental lines (P1 to P10)

Linkage map construction and QTL mapping

The segregation data of 871 polymorphic SNPs identified across the parental lines, were used for the construction of the genetic map (Table 2),for each of the populations separately. The number of markers distributed across the biparental population ranged from 63 to 209. The average inter-marker distance between any pair of adjacent markers, across the populations, ranged from 5 cM and 8 cM. Considering the G×E detected across drought management dataset for most of the observed traits were not substantial, the QTL detected for yield under drought were based on a drought stress management dataset. The details of the QTL detected in individual population are described in Table 4 and Figure 3.

QTL for agronomic traits

In total, 27 and 29 QTL were detected for grain yield and anthesis silking interval across the three managements. QTL for grain yield under waterlogging stress were identified on chromosome 1,3,4,7 and 9, while for drought they were detected on chromosome 1,2,3,6 and 8 and for optimal dataset on chromosome 1,2,3,7 and 9. These QTL explained on an average 0.05-26.0%, 0.8 - 23.0% and 0.5-25.0% of the phenotypic variation, under the three managements, respectively. Among the QTL detected for yield under the three management schemes, most exhibited partial to complete dominance, except for two QTL (GY_D_BP6_1.3, GY_D_BP6_6.2) on chromosome 1 (bin1.07) and 6 (bin 6.05) in BP 6 explaining 11% and 10% phenotypic variation for drought tolerance and increasing 12-13 quintals/ ha. However, the favorable alleles for these two QTL were contributed by the male and the female parent, respectively.

Incidentally, this QTL detected on chromosome 1 in BP 6 (GY_D_BP6_1.3) was congruent to a QTL for grain yield under waterlogging stress (GY_W_BP1_1.2) explaining 10 percent of the observed phenotypic variation. However under this stress, it exhibited over-dominance. The QTL identified on chromosome 6 (GY_D_BP6_6.2) for drought-stress co-segregated with another drought QTL (GY_D_BP6_6.1). Congruent QTL for waterlogging tolerance have also been detected on chromosome 4 (bin 4.06) (GY_W_BP4_4.2 and GY_W_BP1_4.3) in population BP1 and BP4 and on chromosome 9 (bin 9.04) (GY_W_BP2_9.1 and GY_W_BP4_9.2) in population BP2 and BP4 explaining 14-25% and 0.5-3.0% of the phenotypic variation respectively. This QTL on chromosome 9 was also congruent to a QTL for yield under optimal condition [GY_OBP5_9.1&9.2]. Common loci for grain yield under optimal and drought stress [on chromosome 2 (bin 2.03)] managements have also been detected in this study. The favorable alleles for this region were contributed by the female and the male parent respectively.ASI is an important stress response trait. In general, the larger the ASI, the susceptible is the genotype. In the current study heritability of ASI was low for two populations across drought (BP4 and BP5) and waterlogging (BP1 and BP2) stress. Hence, ASI QTL were not detected in these populations. A congruent QTL for drought stress has been identified for ASI on chromosome 7 (bin 7.04) across 2 populations (ASI_D_BP2_7.1; ASI_D_BP7_7.2 &7.3), while a constitutive QTL effecting ASI under drought and optimal condition was detected on chromosome 1 (bin 1.09) [ASI_D_BP2_1.1 and ASI_O_BP7_1.3] in the two populations (BP2 and BP7). As expected, the favorable alleles for these QTL are contributed by drought tolerant parents. Most of the identified QTL for these traits exhibited dominance or overdominance except for one QTL on chromosome 8 (bin 8.02) [ASI_D_BP2_8.1] for drought stress and two QTL one each on chromosome 7 (bin 7.03) [ASI_O_BP1_7.1] and chromosome 10 (bin 10.03) [ASI_O_BP2_10.1] for optimal condition, where the loci were additive.

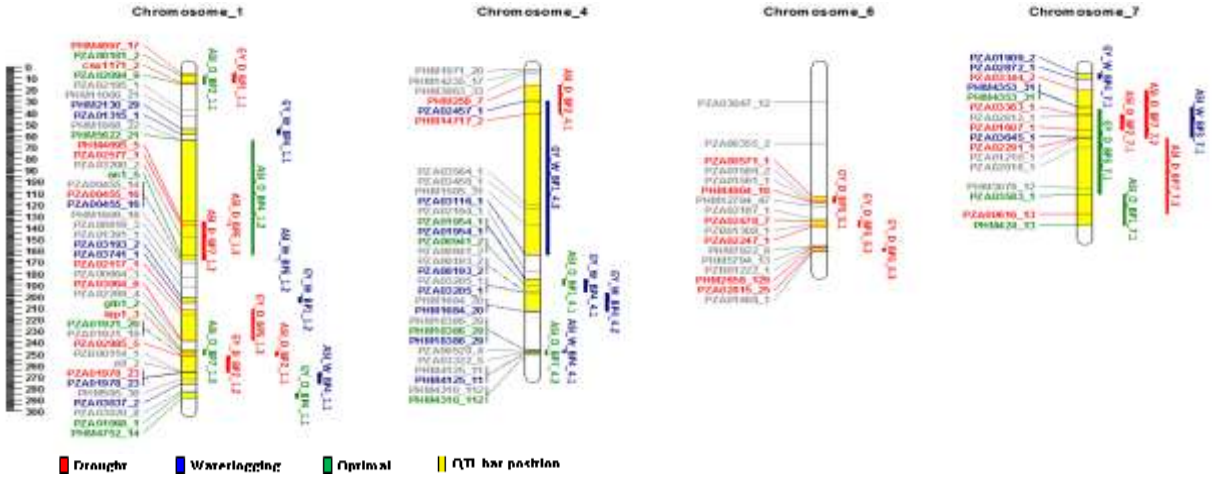

Figure 3. QTL detected on two agronomic responsive traits (GY, ASI) on a $F_{2:3}$ mapping populations

QTL clusters

Two major QTL clusters were observed on chromosome 1 (bin 1.05-1.07) and chromosome 7 (bin 7.01-7.03). The region on chromosome 1 was mainly identified for QTL for ASI and grain yield under drought. Incidentally, this region also identified a QTL for grain yield and ASI under waterlogging management. Second region on chromosome 7 composed of three QTL detected for ASI under drought stress while one QTL each for grain yield and ASI under waterlogging and optimal condition. In addition to these major clusters, two smaller clusters, one on chromosome 4 (bin 4.06-4.08) and one on chromosome 6 (bin 6.05-6.07) seem important, as each of these two regions identified three grain yield QTL for waterlogging and drought tolerance, respectively. However, the favorable alleles for all waterlogging-tolerant QTL were contributed by the female drought tolerant parent and one of the QTL for drought-tolerant QTL received the favorable allele from waterlogging-tolerant female parent.

Discussion

Conventional breeding might be quite time consuming in improving simultaneously both drought and waterlogging tolerance due to the complexities associated with precision phenotyping for these traits. Identification of markers closely linked to genomic regions conferring tolerance to drought and waterlogging could greatly assist in accelerating gains that a breeder could achieve by developing beneficial combinations and targeted manipulations of the genome. Flowering-stage, drought-stress and vegetative-stage waterlogging are the most critical stages in terms of yield loss (Jones and Setter, 2000; Liu et al., 2010; Saini and Westgate, 2000; Zaidi et al., 2004). This study reports a loss of 20-80 percent grain yield across populations under drought and waterlogging stress, as compared to the optimal performance. As expected, the variability for grain yield reduced under the two stresses in general as compared to the optimal management for most populations. However, in a few of the populations, the variability under waterlogging stress was higher. This difference might be due to the fact that a large number of the plants did not yield (Zero yielders), under vegetative-stage waterlogging, suggesting the severity of waterlogging stress.

The complexity of grain yield along with the major role of dominance gene action was observed throughout this study. These findings are in conformity with several previous studies, wherein grain yield have been associated with dominance effect (Nikolic et al., 2013; Sibov et al., 2003). While several QTL have been detected for grain yield, this study identified a common QTL for yield under drought and waterlogging on chromosome 1 (bin 1.07), which is in close proximity to a region (bin 1.06) previously identified for grain yield (Almeida et al., 2013; Ribaut et al., 1997; Tuberosa et al., 2000; 2002;Messmer et al., 2009) and several root traits (Cai et al., 2012; Tuberosa et al., 2002) under water-stressed (drought) environments and hydroponics. A-QTL for root-pulling resistance, has also been identified in this region (Giuliani et al., 2000; Lebreton, 1995). This genomic region has also been identified for several waterlogging responsive traits such as reduced plant height and root length (Osman et al., 2013) and constitutive expression of adventitious root formation (Mano et al., 2007; 2008). A QTL has also been identified in this genomic region for water logging tolerance in an independent RIL population (Babu, pers comm).

Two additional regions of relative importance for grain yield have been identified on chromosome 4 (bin 4.06-4.08) and on chromosome 6 (bin 6.05-6.07) each contributing respectively to waterlogging and drought tolerance. These genomic regions have been identified as partially dominant, except for one of the drought tolerant QTL clearly exhibiting additivity. QTL cluster for several waterlogging response traits have been previously identified on bin 4.07-4.08 (Osman et al. 2013; Zou et al. 2010). This region has also been identified as a region of importance for adventitious root formation above soil in maize (Mano et al., 2005) and to encompass genes actively involved in Abscisic acid synthesis pathways, that functions to inhibit growth and regulate plant stress responses (Osman et al., 2013; Park et al., 2009).

It is interesting to note that a few of the QTL for drought tolerance identified in bins1.02, 1.07 and 3.04, had their favorable alleles contributed by the waterlogging-tolerant female parent. Similarly, favorable alleles for few major important QTL on bin 1.04, 3.07 and 9.04, identified for grain yield under waterlogging stress were contributed by the drought-tolerant male parent. These findings suggest that: i) the parental lines for these traits had favorable and unfavorable alleles dispersed among each other; and/or ii) these regions are adaptive loci for the fitness traits and are being differentially expressed under stress.

ASI is a visual indicator of the reproductive success of a maize crop. Several studies have reported a close association of grain yield with this trait (Edmeades et al., 2000). Abiotic stresses often widen the interval between anthesis and silking in maize, thereby reducing the reproductive capacity of the crop plant and impacting grain yield. Evaluation of historical series of Pioneer hybrids under optimal and water stress condition have revealed an indirect selection of reduced ASI particularly during drought stress (Campos et al. 2005) implicating the importance of this trait. This study revealed several QTL of importance for ASI under drought and waterlogging

stress, most important among them were the regions on chromosome 1 (bin 1.04-1.06), chromosome 3 (bin 3.04-3.05) and on chromosome 7 (bin 7.02). These regions commonly influenced both waterlogging and drought stress. All of these regions were neighboring or adjacent to QTL detected for grain yield under waterlogging and/or drought stress implicating the importance of this trait to abiotic stress tolerance. The opposite effects of the adjacent loci detected for both grain yield and ASI, further confirms the negative linkage between these two traits. Previous studies have also reported a close negative linkage of grain yield with ASI (Bolaños and Edmeades, 1996; Messmer et al. 2009; Ribaut et al., 1997) under drought stress implicating the importance of ASI under water stress. The loci on chromosome 3 (detected in this study) have been previously reported to contains a candidate gene, *Zmm16* involved in reproductive organ development (Dwivedi et al. 2008; Almeida et al. 2013; Setter et al. 2011; Whipple et al., 1997). This study also revealed congruent ASI QTL under drought stress on chromosome 8 and 10. Previous studies have also co-located this region with ASI under drought stress (Almeida et al. 2013, Welcker et al., 2008). In addition, the current study also revealed several QTL for ASI under waterlogging stress such as ones on chromosome 5 (bin 5.07), 6 (bin 6.07) and 8 (bin8.07). While limited literature is available suggesting genomic regions associated with ASI under flooding conditions in maize, the common genomic regions identified here for ASI under both stresses, suggests a common mechanism (at least in part) for this trait.

While several QTL have been identified for drought and waterlogging across populations, this study fails to identify any genomic region that is common across all seven populations. The high density GBS genotypes that are currently being imputed would facilitate a combined genome-wide association study across all populations.

Conclusion

The genomic region identified at chromosome 1 could be used in marker-assisted selection for developing maize genotypes with combined drought- and waterlogging-tolerance. Also, the genomic regions on chromosome 4 and 8, could be used, selectively, for drought and/or waterlogging tolerance.

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Table 4. Description of QTL detected on two agronomic and tree stress responsive traits on a $F_{2:3}$ mapping population

QTL\ Trait	Position cM	Markers		Physical position Left	Physical position Right	Bin position Left	Bin position Right	LOD Score	Additive Effect	Dominant Effect	R2 (%)	*Gene action	Faborable allele
Grain yield (t/Ha)													
GY_D_BP6_1.3	116.9	PZA02117_1	- PZA03064_6	211.84	237.8	1.07	1.08	13	0.13	0.01	11.2	A	WLTP
GY_D_BP5_2.1	0	PZA00590_1	- PZA02450_1	21.42	45.69	2.03	2.04	15	-0.2	0.11	20.5	PD	DTP
GY_D_BP3_3.1	0	PZA00413_20	- PZA02299_16	113.82	90.68	3.05	3.05	14	-0.1	0.29	17.1	OD	DTP
GY_D_BP6_6.2	9.6	PZA02478_7	- PZA02247_1	134.48	139.3	6.05	6.05	13	-0.12	0.01	10.8	A	DTP
GY_D_BP6_6.3	60.2	PHM2658_129	- PZA02815_25	157.79	160.83	6.07	6.08	15	0.13	-0.03	13.6	PD	WLTP
GY_D_BP4_8.1	26.1	PHM15744_10	- PZA02748_3	127.96	109.76	8.05	8.05	19	-0.14	0.14	22.8	D	DTP
GY_O_BP4_2.1	0	PZA00224_4	- vdac1a_1	170.45	168.3	2.06	2.06	16	0.27	-0.06	14.7	PD	WLTP
GY_O_BP5_2.2	3	PZA00590_1	- PZA02450_1	21.42	45.69	2.03	2.04	23	-0.38	0.08	26.5	PD	DTP
GY_O_BP7_3.1	24.6	PHM13742_5	- PZA02665_2	205.96	218.19	3.08	3.09	13	-0.33	0.15	26	PD	DTP
GY_W_BP4_1.1	14.9	PHM2130_29	- PZA01315_1	54.35	59.27	1.04	1.04	17	-0.17	0.17	17.3	D	DTP
GY_W_BP1_1.2	73.7	PZA03193_2	- PZA03741_1	200.75	205.52	1.07	1.07	12	0.07	-0.18	9.6	OD	WLTP
GY_W_BP4_4.1	29.6	PZA01954_1	- PZA00193_2	185.31	196.28	4.06	4.08	22	-0.31	0.12	25.3	PD	DTP
GY_W_BP4_4.2	37.8	PZA03205_1	- PHM1684_20	197.07	213.27	4.08	4.08	20	-0.28	0.08	20.7	PD	DTP
GY_W_BP4_7.1	24.4	PZA02872_1	- PZA01909_2	11.08	6.54	7.01	7.01	16	-0.19	0.2	19.8	D	DTP
Anthesis Silking Interval (days)													
ASI_D_BP2_1.1	6	kip1_3	- PZA02985_5	248.46	252.11	1.09	1.09	12	0.38	-0.51	10.2	OD	DTP
ASI_D_BP2_7.1	0	PZA03363_1	- PZA01607_1	41.57	55.01	7.02	7.02	25	0.53	-0.59	19.5	OD	DTP
ASI_D_BP2_8.1	0	PZA01079_1	- PHM5158_13	14.61	18.19	8.02	8.02	17	0.6	-0.09	11.4	PD	DTP
ASI_D_BP6_8.2	39.6	PHM3856_10	- PZA02683_1	84.87	74.72	8.03	8.03	17	0.84	-0.81	22.9	A	DTP
ASI_D_BP6_10.1	59.7	PZB01111_8	- PZA02663_1	118.41	119.87	10.04	10.06	13	0.8	-0.82	20.8	D	DTP
ASI_O_BP2_1.1	19.9	PZA02094_9	- PZA00181_2	15.33	8.17	1.02	1.01	14	-0.85	0.52	18.5	D	WLTP
ASI_O_BP7_1.3	76.9	PZA01921_20	- glb1_2	250.99	246.65	1.09	1.09	14	0.16	-1.31	11.4	OD	DTP
ASI_O_BP6_3.1	0	PZD00038_2	- PZA00749_1	4.65	6.93	3.03	3.02	13	0.44	-0.61	14.9	OD	DTP
ASI_O_BP1_7.1	20.7	PHM424_13	- PZA03583_1	138.09	111.08	7.04	7.03	12	0.53	-0.09	9.7	D	DTP
ASI_W_BP4_1.1	43.9	PZA01978_23	- PZA03037_2	266.5	275.99	1.1	1.11	20	-1.28	-0.28	12.8	PD	WLTP
ASI_W_BP6_1.2	79.5	PZA00455_16	- PZA00455_16	168.71	168.71	1.06	1.06	13	0.07	-0.68	9.1	PD	DTP
ASI_W_BP6_3.1	21.4	PZA00508_2	- PHM2343_25	11.34	26.85	3.04	3.04	12	0.33	-0.58	14.1	OD	DTP
ASI_W_BP7_5.1	6.1	PHM5359_10	- PZB00054_3	3.6	7.58	5.01	5.01	12	-0.73	0.39	20	OD	WLTP
ASI_W_BP3_7.1	1.3	PHM4353_31	- PZA03645_1	35.22	61.42	7.02	7.02	12	-0.35	1.64	9.2	D	WLTP

*Gene action: A=Additive; PD=Partially dominant; D=Dominant; OD=Overdominant. $ Favorable allele: WLP: Waterlogging tolerant parent; DTP: Drought tolerant parent