

Retraction Notice

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History

Expression of Concern:

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Correction:

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Comment:

The paper does not meet the standards of "Agricultural Sciences".

This article has been retracted to straighten the academic record. In making this decision the Editorial Board follows COPE's [Retraction Guidelines](#). The aim is to promote the circulation of scientific research by offering an ideal research publication platform with due consideration of internationally accepted standards on publication ethics. The Editorial Board would like to extend its sincere apologies for any inconvenience this retraction may have caused.

Editor guiding this retraction: Prof. Daniele De Wrachien (EiC of AS).

Please see the [article page](#) for more details. The [full retraction notice](#) in PDF is preceding the original paper which is marked "RETRACTED".

RETRACTED

Genetic Dissection of Pre-Flowering Growth and Development in *Sorghum bicolor* L. Moench under Well-Watered and Drought Stress Conditions

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Abstract

The goal of the present study is to identify QTL regions influencing pre-flowering drought tolerance and agronomic performance of sorghum under early season drought stress conditions. The random occurrence of drought after sowing leads to reduced growth rates and delayed flowering and harvest time. A good rooting system and high leaf areas are required to acquire water from the soil and facilitate a high level of assimilation production during stress cycles and during recovery following each stress cycle. A RIL population was grown in pots under controlled-environment conditions. Experiments included a treatment in which plants were cultivated in a continuously drying soil and a well-watered control. Drought stress was induced by withholding irrigation water from the plants for three to four weeks after sowing. Plants were harvested prior to flowering and leaf area, leaf, stem and root dry weights, root lengths and water consumption were measured. Composite interval mapping was performed for 13 traits and significant QTL were claimed at LOD > 2.5. A total of 50 QTL were detected on ten chromosomes or 14 linkage groups, respectively. The most promising regions for good agronomic performance under pre-flowering drought stress were identified on chromosomes SBI-01, SBI-02, SBI-05 and SBI-06. While QTL hotspots on SBI-01 and SBI-02 affected mainly vegetative traits, some regions on SBI-05 and SBI-06 have large effects on yield and yield components. Co-localizations of yield-related parameters and vegetative traits on SBI-05 support the hypothesis that high leaf area production under drought stress is directly related to increasing yields under stress.

Keywords

Grain Sorghum, Drought Stress, Vegetative Growth, Water Use Efficiency, QTL

1. Introduction

Sorghum bicolor (L.) Moench is predominantly grown in arid and semi-arid environments. Grain sorghum is highly tolerant to drought. However, pre-flowering drought leads to reduced growth rates and delayed flowering. As a consequence, harvest time is largely delayed as well, which makes the crop more vulnerable to drought stress during grain filling and maturation as well as more vulnerable to pest attack. Grain sorghum is generally sown at the beginning of the rain season in semi-arid regions. The sorghum growing seasons in Sub-Saharan Africa are regionally characterized by initial rainfalls with subsequent periods of drought. Delayed harvest time occasionally leads to food shortages. A crop with high plant vigor and growth rates during early development stages may be advantageous under conditions affected by early season drought [1]. A good rooting system can acquire soil water and nutrients from deeper layers, and high water-use efficiencies (WUE) minimize the amount of soil water consumed per unit of above-ground dry matter produced. Similarly, promoting early canopy development increases CO₂ assimilation rates per ground area during later growth stages.

Research for improving drought tolerance of sorghum has mainly focused on post-flowering traits. In the USA, for example, the majority of commercial sorghum hybrids grown under non-irrigated conditions were considered to have considerable pre-flowering drought tolerance but no significant post-flowering drought tolerance. Premature senescence leads to substantial yield losses under drought stress and stay-green, the ability to maintain green leaf area in conditions of limited soil water availability, contributes largely to post-flowering drought tolerance in sorghum [2]. Quantitative trait loci (QTL) for post-flowering drought tolerance, including the stay-green trait, have been described in numerous studies [3]-[7]. Maintenance of green leaf area under drought stress during kernel development not only increases yields but also reduces the risk of fungal diseases [8] [9]. Rate of senescence was found to be more important than onset of senescence for the stay-green phenotype [10]. Gene-derived microsatellite markers improving marker-assisted selection (MAS) possibilities for the stay-green trait were developed and mapped [11]. Drought stress EST-derived microsatellite loci were mapped by [12].

Probably due to the fact that sorghum in comparison to other crops is less sensitive to drought *per se*, and that a single trait like stay-green could substantially improve yields under unfavorable conditions, relevant improvement of traits influencing growth prior to anthesis has been widely neglected in the past decade. However, QTL mapping studies on pre-flowering drought tolerance were first reported by [13]. Kebede *et al.* (2001) [6] detected four QTL for rating scores for pre-flowering drought tolerance, which, among others, were based on leaf rolling. The transcriptome response of root and shoot tissue of sorghum seedlings to osmotic stress was analyzed and revealed both overlapping and distinct responses to salinity and osmotic stress [14]. Important traits like WUE and root growth have not been considered for QTL analysis to date.

The objectives of the present study were: (1) to identify QTL regions affecting leaf area development, dry matter production, root growth and water-use efficiency in sorghum subjected to drought stress conditions prior to flowering; and (2) to detect QTL regions for yield and yield components after the pre-flowering drought stress treatment.

2. Materials and Methods

2.1. Plant Material and Genotyping

A recombinant inbred line (RIL) population comprised of 140 RILs was developed at the Grain Crops Institute, Potchefstroom, South Africa, from a cross between a high yielding parental line (HYP) and a breeding line described as drought tolerant (DTP). The DTP shows less wilting and leaf rolling under drought stress and develops more roots than the HYP. Progeny of the cross were advanced to F₅ by single-seed descent. Phenotyping was conducted on 100 RILs in the first three experiments and 140 RILs in the fourth and fifth experiments.

DNA was extracted from leaf tips of F₅ seedlings using the cetyl trimethylammonium bromide (CTAB) me-

thod. Genotyping was carried out at Diversity Arrays Technology Pty. Ltd. (DArT), Yarralumla, Australia. 184 polymorphic markers were chosen for RIL fingerprinting. Nine informative expressed sequence tag (EST)-derived simple sequence repeat (SSR) markers [15] were used in addition to the DArT markers. Polymerase chain reaction (PCR) was carried out on a T-Gradient PCR machine (Biometra, Göttingen, Germany). DNA was denaturalized at 94°C for 10 min. The PCR protocol had a denaturation temperature of 94°C, an annealing temperature of 52°C and a polymerization temperature of 72°C. The first 25 cycles with 30s for each step were followed by eight cycles with extended annealing (45 s) and polymerization (60 s) times. We used DY-682 labeled M13 primers in the PCR reactions (Eurofins MWG, Ebersberg, Germany). Amplification products were separated by polyacrylamide gel electrophoresis using an LI 4200 sequencer (Licor Inc., Lincoln, USA).

Marker positions were taken from a consensus map published by [16]. The selected markers cover 1183.1cM with an average marker distance of 9.5 cM.

2.2. Experimental Setup and Phenotyping

The first two experiments and the fourth experiment comprised a well-watered (ww) treatment and plants grown in a continuously drying soil (cd). The third experiment included only the cd treatment. Experiment four included two subsequent stress cycles. Plants were re-watered at the end of the first stress cycle to 50% of the maximum water-holding capacity (WHC) of the soil. All experiments were carried out in a greenhouse (Figure 1). Plants were sown in 12.5 cm × 50 cm polyvinyl chloride pots filled with 9.4 kg dry sandy soil and 1100 ml nutrient solution, which corresponds to 80% of maximum soil WHC. The two plants per pot were thinned to single plants after emergence and each experiment was comprised of replicates per treatment and RIL or parental line, respectively. Plants were fertigated with 0.15% Scotts Universal Orange (Scotts, Marysville, Ohio, USA) fertilizer solution (NPK 16:6:26) twice a week. Water consumption was estimated by weighing the pots before fertigation to 80% WHC and during the stress cycle. Evapotranspiration was minimized by covering the soil with 200 g of gravel. Irrigation was withheld from the cd treatment when most plants were at the six leaf stage. Climate data and soil water status during experiments is shown in Table 1. In order to avoid nutrient deficiencies in the control treatment, the total amount of fertilizer applied to ww and cd was not the same.

Plants were harvested 12 hours after re-watering at the end of stress cycles. Re-watering was done when the lower leaves of the most susceptible recombinant inbred lines (RIL) showed clear wilting symptoms but before the first leaves were falling off. Leaf area (LA) was measured using the LI-3100 area meter (Licor Inc., Lincoln, NE, USA). Roots were washed carefully, placed in a water bath and scanned with a flatbed scanner. Total root lengths (TRL) were measured using WinRhizo (Regent Instruments Inc., Quebec, Canada). The dry weights of roots, leaves and stems were measured after drying the plant parts at 105°C until weight constancy.

The fifth experiment included all 140 RILs and a continuously drying soil as well as a well-watered treatment. As in experiment four, cultivation practices were the same and plants were subjected to two drought stress cycles. The second stress cycle ended after flowering. Seed number (NSE) per panicle was counted and yield (YLD), as well as hundred kernel weights, was measured (HKW). Panicle initiation was counted in the number of days from sowing to heading (PIN).

Table 1. Duration of stress cycles, daily mean, maximum and minimum temperatures (T) and relative humidity (RH) during experiments and average soil water status of plants grown under drought stress expressed as percentage of maximum water holding capacity (WHC) at the end of the stress cycle.

Experiment	1 (2008)	2 ^a (2008)	3 (2009)	4 (2010)	5 (2011)
Sowing date	April 18	Sept. 11	April 8	March 26	May 2
Harvest date	May 30	Nov. 11	May 26	May 22	July 28
Stress cycle duration (day)	21	43	28	18/9	16/8
T (°C) mean (max/min)	21 (25/16)	-	21 (26/16)	22 (26/18)	23 (28/19)
RH (%) mean (max/min)	49 (63/37)	-	52 (68/38)	49 (58/38)	52 (71/31)
% WHC	15	17	8	38/8	36/10

^aClimate data of experiment 2 is not available.



Figure 1. Experiments in the green house.

2.3. Data Analysis

Statistical data analysis was carried out using SAS 9.2 [17]. Means were computed from the two replicates per RIL, treatment and experiment. Root-to-shoot ratio (RSR) was calculated as the ratio between root dry weight (RDW) and shoot dry weight (SDW). Total dry weight (TDW) was measured by RDW plus SDW. Specific leaf area (SLA) was calculated as ratio between leaf area (LA) and leaf dry weight (LDW). Water use efficiency (WUE) was estimated as follows:

$$WUE = (LDW + SDW + RDW) / WC$$

where WC is the amount of water consumed. Since not all RILs were used in all experiments and dry weights and LAs among experiments were different, due to the fact that the stress cycle duration was highly affected by temperature and radiation during experiments, results were converted into relative values in relation to HYP (HYP = 100). Pearson's correlation coefficients between relative trait values were estimated. Means were separated by subjecting relative trait values to analysis of variance (ANOVA) with the following model:

$$y_{ij} = \mu + \tau_i + \beta_j + \epsilon_{ij}$$

where μ is the population mean, τ_i is the effect of the *i*th RIL, β_j is the effect of the *j*th experiment and ϵ_{ij} is the random error of the *i*th RIL and in the *j*th experiment. Broad sense heritability (h^2) was estimated as:

$$h^2 = \sigma_G^2 / (\sigma_G^2 + \sigma_{G \times E}^2 (1/e) + \sigma^2 (1/re))$$

where σ_G^2 is the genotypic variance, $\sigma_{G \times E}^2$ is the genotype x environment interaction variance, σ^2 is the error variance, *e* is the number of environments and *r* is the number of replications.

The genetic map was computed with JoinMap 4 [18] and the multipoint maximum likelihood mapping function [19]. QTL analysis was carried out using PLABQTL 1.2 [20] using the composite interval mapping method [21] by multiple regression with cofactors [22]. A liberal threshold logarithm of the odds (LOD) score of 2.5 was used for claiming the presence of a QTL in order to minimize the number of undetected QTL.

3. Results

Mean trait values of parental lines and relative means of DTP and the RIL population are shown in **Table 2**. HYP had higher LA and LDW as DTP and as the RIL population under both growing conditions. DTP surpassed SDW and TDW of HYP and the RIL mean under drought stress. This also held true for RDW. RSR and WUE of DTP were higher if compared to HYP. Differences among RILs of all traits, except TRL (cd) and WUE (cd), were at least highly significant ($p < 0.01$). No significant variability within RILs was found for SLA (cd). Except for RSR (cd), h^2 was always higher for traits measured in the ww environment. Highest heritabilities were found for SDW (ww) and TDW (ww). Heritability of SLA (cd) and WUE (cd) was extremely low (**Table 2**). NSE was largely reduced in the cd treatment. Correlation between treatments was 0.24. There was high variation in NSE in both treatments. HKW was not influenced as much by drought stress. Correlation between treatments was 0.74.

Frequency distributions of SLA (cd) and WUE (cd) show that there was not much variation within the population (**Figure 3**). Interestingly, the variation among RILs under ww conditions was in most cases at least on the same level or even higher as in the drought stress conditions. Reduced variation among RILs in cd was most ob-

Table 2. Descriptive statistics and analysis of variance for 13 traits under well-watered (ww) conditions and continuously drying soil (cd) in the green house.

Trait ^a	Unit	Parental lines			RIL population					
		HYP	DTP	Mean	SD ^b	Min	Max	h ²		
				%		%				
LA (ww)	cm ²	1319	1031	78.1	89.3	***c	19.9	35.5	127.7	0.55
LA (cd)	cm ²	768	710	92.5	91.4	**	15.6	45.5	125.6	0.37
LDW (ww)	g	5.22	3.91	75.0	91.6	***	22.4	28.5	137.4	0.66
LDW (cd)	g	3.37	3.01	89.2	88.8	***	14.3	46.6	119.5	0.63
SDW (ww)	g	4.43	3.71	83.7	104.7	***	24.8	24	163.1	0.79
SDW (cd)	g	2.26	2.79	123.5	112.5	***	19.1	74.6	177.7	0.55
RDW (ww)	g	2.04	2.41	118.1	108.9	***	35.8	11	205.5	0.55
RDW (cd)	g	1.58	1.85	117.1	105	***	19.9	46.7	151.9	0.44
TDW (ww)	g	11.69	10.03	85.8	99.6	***	19.5	23.8	131.8	0.77
TDW (cd)	g	7.21	7.65	106.0	99.3	***	11	67.4	123.3	0.51
TRL (ww)	cm	4311	4090	94.9	124.2	**	27.8	65.3	183.6	0.57
TRL (cd)	cm	5731	5933	103.5	103.5	*	9.3	76.3	126.2	0.33
RSR (ww)	g·g ⁻¹	0.21	0.28	130.4	110.8	***	26	41.9	203	0.31
RSR (cd)	g·g ⁻¹	0.31	0.34	110.7	107.4	***	18.2	64.5	172.9	0.54
SLA (ww)	cm ² ·g ⁻¹	266	266	100.2	99.2	***	7.7	83.1	124.3	0.45
SLA (cd)	cm ² ·g ⁻¹	220	230	104.5	102.9	n.s.	6.8	87.1	118.6	0.07
WUE (ww)	g·l ⁻¹	5.13	6.01	117.3	115.5	***	17.2	63.2	163.1	0.63
WUE (cd)	g·l ⁻¹	6.19	7.28	117.6	102.3	*	7.4	79.4	119.7	0.15
PIN (ww)	DAS ^d	65	59	-	61.4	**	2.9	47	79.5	0.74
PIN (cd)	DAS	61.5	60	-	64.8	**	2.4	51.5	80	0.76
NSE (ww)	seed	903	495	-	724	**	202	100	1527	0.34
NSE (cd)	seed	536	421	-	394	**	112	100	759	0.22
HKW (ww)	g	2.07	1.52	-	1.88	**	0.37	0.56	3.51	0.66
HKW (cd)	g	1.97	1.47	-	1.58	**	0.38	0.39	3.59	0.61
GYL (ww)	g·plant ⁻¹	17.78	7.32	-	13.6	**	3.90	5.00	23.2	0.38
GYL (cd)	g·plant ⁻¹	10.37	6.71	-	5.49	**	1.71	2.92	9.9	0.36

^aTrait abbreviations are leaf area (LA), leaf dry weight (LDW), shoot dry weight (SDW), root dry weight (RDW), total dry weight (TDW), total root lengths (TRL), root to shoot ratio (RSR), specific leaf area (SLA), water use efficiency (WUE), panicle initiation (PIN), hundred kernel weight (HKW), number of seed per panicle (NSE) and grain yield (GYL). ^bSD = standard deviation. ^cMeans followed by *, ** or *** indicate statistical differences among RILs on the 0.05, 0.01 or 0.001 probability level. ^dDAS = days after sowing.

vious for LDW, TDW and TRL (Figure 3).

Most of the traits were positively correlated with each other (Table 3). All the traits had positive correlations between well-watered and drought stress conditions at $p < 0.01$. The strongest correlation was found for PIN ($r = 0.81$). High correlations between LA and LDW ($r = 0.94$ in ww and $r = 0.91$ in cd) reflect the missing variation in SLA (Table 3). RDW was significantly correlated to LA, LDW and SDW (ww) but not to SDW (cd). Grain yield was positively correlated to all of the yield component traits but PIN was negatively correlated to GYL (ww). Correlations between grain yield and PIN in this study were very interesting for breeding since the single line that has early panicle initiation will have higher grain yield

We detected 50 QTL for 13 traits (Table 4). QTL were detected on all LGs except SBI-05c, SBI-07 and SBI-09a. Only one QTL was detected on each of SBI-08 and SBI-10. 10 QTL were located on SBI-06, 10 on SBI-02, 8 QTL on SBI-01 and 6 QTL on each SBI-03, SBI-05 and SBI-10 (Figure 2). Five QTL for traits evaluated under drought stress were identified on SBI-01 and two on SBI-02. Most QTL detected on SBI-06 were for traits



Figure 2. Genetic linkage map and significant additive QTL for agronomic traits and yield components of 140 RILs and their parents grown in the green house. Trait abbreviations are leaf area (LA), leaf dry weight (LDW), shoot dry weight (SDW), root dry weight (RDW), total dry weight (TDW), total root lengths (TRL), root to shoot ratio (RSR), specific leaf area (SLA), water use efficiency (WUE), panicle initiation (PIN), seed number (NSE), hundred kernel weight (HKW), and yield (YLD) under well-watered conditions (filled boxes) and in a continuously drying soil (open boxes). QTL are claimed at LOD > 2.5. Boxes show LOD peaks ± 2 cM. Whiskers give the LOD > 2 confidence intervals. Marker positions are given according to Mace *et al.* (2009).

measured in the well-watered control. QTL for LDW (ww), RDW (ww), TDW (ww), PIN (ww), LA (cd), LDW (cd) and RDW (cd) were clustering on SBI-02 at marker sPbn-2229. QTL for LA (ww), YLD (ww), HKW (ww), PIN (ww), PIN (cd), HKW (cd), YLD (cd) clustered on SBI-06 between markers sPbn-2404 and sPbn-4036.

While many QTL were detected only in the ww or cd treatment, virtually perfect constitutive QTL (*i.e.* QTL appearing at identical positions under both non-stress and stress conditions) were identified for HKW and YLD on SBI-06. QTL positions for HKW on SBI-01, RDW and LDW on SBI-02, and PIN on SBI-06 give hints of a constitutive nature as well.

4. Discussion

The DArT markers used in the present study turned out to be an affordable high throughput marker system, powerful for QTL detection. The use of DArT makes sense in crops like sorghum since SNP arrays are not publicly available. However, the already described non-random patterns of marker distribution [16] resulted in large gaps on most of the chromosomes. The use of additional marker systems like microsatellites would be necessary to fill

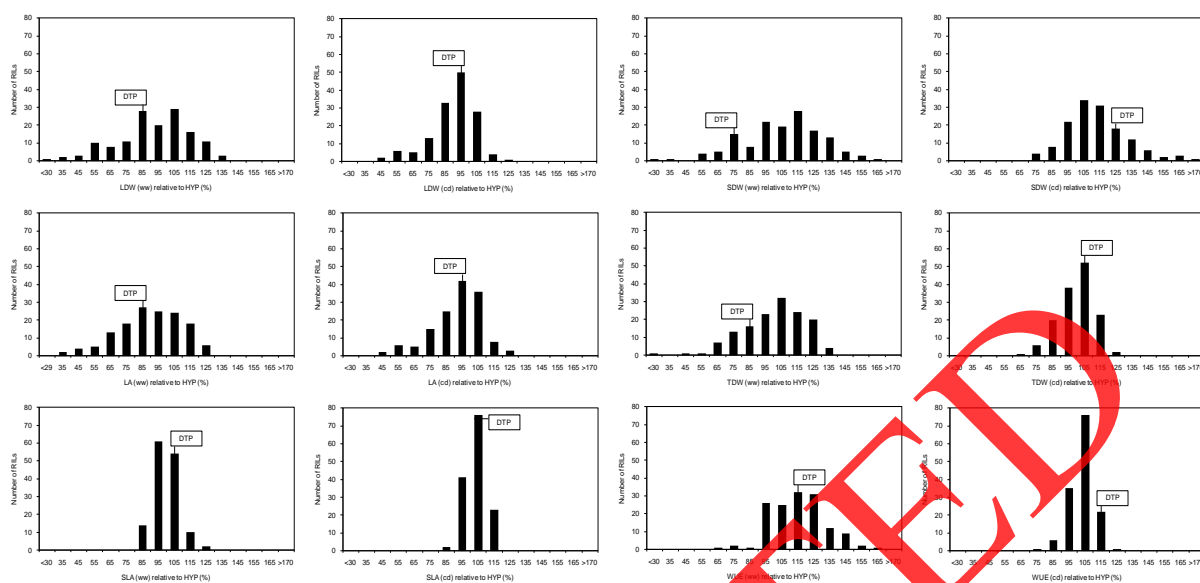


Figure 3. Frequency distributions of agronomic traits and yield component of 140 RILs and their parents grown in the green house. Trait abbreviations are leaf dry weight (LDW), shoot dry weight (SDW), leaf area (LA), total dry weight (TDW), specific leaf area (SLA), water use efficiency (WUE), root dry weight (RDW) under well-watered conditions (ww) and in a continuously drying soil (cd). Values of 140 RILs and the drought tolerant parental line (DTP) are shown as percentage of the high yielding parental line (HYP = 100).

the gaps and provide equal genome coverage. The to-date relatively seldom usage of DArT markers for QTL detection makes comparisons with previously published QTL for drought tolerance in sorghum somewhat difficult.

We identified a major QTL group on SBI-02b at sPbn-2229 with LOD peaks at 0 and 2 cM from the top of the LG. Srinivas *et al.* (2009) [12] mapped seven out of 28 drought stress EST-derived microsatellite markers on SBI-01. Close to one of them (Dsenhsm66) is QTL for PIN. QTL for several agronomic traits, including leaf number and leaf area at anthesis of sorghum RILs irrigated prior to flowering, were previously detected on SBI-01 by [15]. Several of the QTL were linked to *Xtp43* (leaf and tiller number) and *Xtp32* (days to anthesis and maturity, leaf and tiller number). *Dsenhsm66* was mapped in between the flanking markers *Xtp88* and *Xtp43* [15].

Kebede *et al.* (2001) [6] described a QTL group including QTL for pre-flowering drought tolerance and stay-green on linkage group (LG) G following the classification of [4]. LG G corresponds to SBI-01, according to [23]. QTL for seedling emergence and vigor under low temperatures were mapped on SBI-01 close to the microsatellite marker *Xtp43* [24] [25]. The QTL was located 72 cM from the top of SBI-01. The map of [16] includes above-mentioned microsatellite markers and shows that the nearest markers of QTL positions of the QTL group relevant for traits under drought stress (sPbn-0232 and sPbn-0274) are located between the microsatellite loci *Xtp88* and *Xtp32*. The QTL hotspot on SBI-01 is several cM upwards of those markers; however, fine mapping of this region could facilitate the construction of stable QTL markers suitable for marker-assisted selection (MAS).

According to our knowledge, QTL for sorghum root traits have not been published to date. However, Tuberosa *et al.* (2002) [26] detected QTL for root characteristics of maize in hydroponics. At least four of the QTL were linked to restricted fragment length polymorphism (RFLP) markers mapped in the sorghum consensus map [16]. The markers *umc5*, *umc44* and *umc38*, which were linked to root weight and root diameter in maize, were mapped on SBI-02, SBI-006 and SBI-09. RFLP marker *umc5* was located approximately 20cM upwards of sPbn-2229 within the support interval of the RDW (ww) and RDW (cd) QTL on SBI-02 identified in the present study. The confidence interval of RDW (ww) on SBI-06 includes the position of *umc44*, approximately 26 cM upwards of sPbn-4732 in the consensus map [16]. sPbn-8954 was mapped several cM downwards of sPbn-4732. sPbn-6089, the nearest marker of the RDW (ww) QTL on SBI-09, falls within the region, to which *umc38* was mapped. Further studies discovering the symphony between maize and sorghum QTL regions are needed to reveal if root traits are possibly regulated by the same genes.

Table 3. Pearson's correlation among 10 traits analyzed under well-watered (ww) conditions and continuously drying soil (cd) in the green house.

	LA ^a (ww)	LA (cd)	LDW (ww)	LDW (cd)	SDW (ww)	SDW (cd)	RDW (ww)	RDW (cd)	TRL (ww)	TRL (cd)	WUE (ww)	WUE (cd)	PIN (ww)	PIN (cd)	HKW (ww)	HKW (cd)	NSE (ww)	NSE (cd)	GYL (ww)	
LA (cd)	0.65** ^b																			
LDW (ww)	0.94**	0.72**																		
LDW (cd)	0.68**	0.91**	0.76**																	
SDW (ww)	0.10	0.04	0.20*	0.08																
SDW (cd)	-0.34**	-0.11	-0.24**	-0.05	0.55**															
RDW (ww)	0.68**	0.24**	0.65**	0.29**	0.41**	-0.13														
RDW (cd)	0.44**	0.52**	0.49**	0.58**	0.28**	0.12	0.37**													
TRL (ww)	0.46**	0.15	0.54**	0.20*	0.67**	0.18	0.71**	0.38**												
TRL (cd)	0.40**	0.29**	0.38**	0.40**	0.21*	0.03	0.34**	0.51**	0.31**											
WUE (ww)	0.63**	0.55**	0.73**	0.57**	0.57**	0.14	0.55**	0.49**	0.58**	0.24**										
WUE (cd)	0.15	0.47**	0.21**	0.47**	0.22**	0.47**	0.01	0.60**	0.07	0.11	0.31**									
PIN (ww)	0.55**	0.41**	0.47**	0.40**	-0.34**	-0.55	0.18	0.25**	-0.03	0.17	0.17*	-0.00								
PIN (cd)	0.57**	0.38**	0.46**	0.34**	-0.41**	-0.61**	0.24**	0.27**	-0.07	0.17	0.13	-0.01	0.81**							
HKW (ww)	-0.43**	-0.36**	-0.39**	-0.36**	0.51**	0.61**	-0.10	-0.11	0.03	-0.12	-0.07	0.07	-0.63**	-0.76**						
HKW (cd)	-0.52**	-0.39**	-0.45**	-0.37**	0.40**	0.61**	-0.15	-0.13	-0.03	-0.23*	-0.15	0.09	-0.88**	-0.79**	0.73**					
NSE (ww)	-0.01	0.10	0.01	0.09	0.00	0.07	-0.06	-0.04	0.05	-0.09	0.00	0.00	-0.25**	-0.24**	-0.02	0.10				
NSE (cd)	0.15	0.14	0.11	0.10	-0.31**	-0.38**	0.04	-0.06	-0.01	0.13	0.00	-0.14	0.34**	0.34**	-0.46**	-0.52**	0.24**			
GYL (ww)	0.26**	0.10	0.21*	0.10	0.39**	0.50**	-0.12	0.02	0.07	0.14	0.00	0.10	-0.58**	-0.67**	0.61**	0.56**	0.73**	-0.18*		
GYL (cd)	0.34**	0.21*	0.32**	0.23**	0.16	0.24**	0.08	0.14	0.00	0.18	0.12	0.05	-0.60**	-0.52**	0.37**	0.50**	0.42**	0.35**	0.55**	

^aTrait abbreviations are leaf area (LA), leaf dry weight (LDW), shoot dry weight (SDW), root dry weight (RDW), total root lengths (TRL), water use efficiency (WUE), panicle initiation (PIN), hundred kernel weight (HKW), number of seed per panicle (NSE) and grain yield (GYL). ^bCorrelations between traits are statistically significant on the 0.05 (*) or 0.01 (**) probability level.

The alleles increasing dry matter production and leaf area of above plant ground parts came in most cases from DTP and HYP. In the case of root traits, the DTP allele on SBI-06 increased RDW under non-stress conditions and decreased RDW on SBI-02. The RDW QTL directly co-localizes with QTL for above-ground plant parts on SBI-02. However, it would be speculative to assume an influence of root growth on water uptake and crop growth from the present study since the rooting zone in pot experiments is strictly limited. Field experiments have to be carried out in order to evaluate if root QTL overlap with grain yield QTL under stress conditions.

QTL for WUE (cd) on SBI-01 overlap only with a QTL for PIN in the present study. The HYP allele increased WUE on the QTL positions. Rice QTL for carbon isotope discrimination were found to be associated to WUE and co-localized with a QTL for leaf length on rice chromosome 1 [27]. Kato *et al.* (2008) [28] detected a QTL for specific water use on rice chromosome 2. The same locus increased relative growth rate of rice seedlings and it was speculated that regulation of dry matter growth partially may be mediated by transpiration processes.

According to Bunce (2010) [29], maize transpiration efficiencies are often lower than potentially possible for C4 species and identified significant variation in leaf transpiration efficiencies of maize lines. Hund (2009) [30] found differences in WUE between drought-susceptible and drought-tolerant maize lines. The susceptible line showed higher stomatal conductance and lower leaf carbon exchange rates at the same time. Thus, inefficient stomatal regulation could lead to luxury consumption of water and the identification of stable markers for transpiration efficiencies could be a major challenge in breeding for drought prone areas.

Table 4. Quantitative trait loci (QTLs) detected for 13 traits analyzed under well watered conditions (ww) and in a continuously drying soil (cd) in the green house.

Trait	Chro.	Position (cM)	Nearest marker	LOD > 1 interval	LOD	R ² (%)	Additive effect
LA (ww)	SBI-01b	68	sPbn-2958	62 - 82	3.17	10.2	7.26
	SBI-06	8	sPbn-7660	6 - 10	5.41	16.8	7.25
LA (cd)	SBI-02	28	sPbn-7317	26 - 30	3.18	10.3	8.82
	SBI-02b	2	sPbn-2229	0 - 10	4.72	16.2	-7.29
	SBI-05	8	sPbn-2880	6 - 12	3.97	13.2	-8.64
LDW (ww)	SBI-02b	2	sPbn-2229	0 - 8	5.67	19.1	-10.35
LDW (cd)	SBI-02	38	sPbn-1617	36 - 42	3.42	11.1	-7.61
	SBI-02b	4	sPbn-2229	0 - 12	3.96	13.8	-5.19
	SBI-03b	0	sPbn-9139	0 - 8	2.63	9.0	3.71
	SBI-05	8	sPbn-2880	6 - 14	2.84	9.6	-7.02
SDW (ww)	SBI-10	36	sPbn-9999	18 - 52	2.63	8.6	8.11
SDW (cd)	SBI-01b	46	sPbn-7173	28 - 58	3.38	11.0	-6.09
RDW (ww)	SBI-02	4	Dsenhsbm25	0 - 14	2.85	10.1	-10.92
	SBI-06	112	sPbn-0017	100 - 116	3.57	11.6	10.86
	SBI-09b	34	sPbn-6089	22 - 44	2.63	8.6	8.90
RDW (cd)	SBI-02b	0	sPbn-2229	0 - 10	3.23	11.4	-6.59
TDW (ww)	SBI-02b	0	sPbn-2229	0 - 10	3.04	10.8	-6.14
	SBI-06	104	sPbn-1972	90 - 116	3.92	12.6	7.38
TDW (cd)	SBI-01b	42	sPbn-7173	30 - 50	3.57	11.5	-3.59
	SBI-09b	30	sPbn-6089	18 - 50	2.99	9.7	3.64
TRL (ww)	SBI-05b	0	sPbn-4806	0 - 12	3.43	15.8	-8.79
RSR (ww)	SBI-03	70	sPbn-5594	62 - 72	3.34	10.8	-9.40
	SBI-03	132	Dsenhsbm31	124 - 134	3.91	16.3	14.4
	SBI-04b	38	sPbn-7315	32 - 40	2.83	9.2	-17.48
SLA (ww)	SBI-05	0	sPbn-4041	0 - 2	4.92	17.1	-3.79
SLA (cd)	SBI-03	126	Dsenhsbm31	116 - 134	6.51	25.7	-3.61
WUE (cd)	SBI-01	52	sPbn-6007	46 - 58	2.91	9.5	6.31
HKW (ww)	SBI-01b	66	sPbn-2958	54 - 82	3.36	12.2	-0.22
	SBI-04	0	sPbn-9359	0 - 2	3.77	13.7	-0.23
	SBI-06	12	sPbn-4036	8 - 22	4.69	16.6	-0.24
	SBI-08	62	sPbn-0380	44 - 74	2.54	9.4	0.21
HKW (cd)	SBI-01b	72	sPbn-2958	46 - 90	2.85	10.2	-0.28
	SBI-04	0	sPbn-9359	0 - 2	2.63	9.5	-0.23
	SBI-06	12	sPbn-4036	8 - 26	5.33	18.2	-0.32
NSE (ww)	SBI-02	52	sPbn-6724	44 - 64	2.59	9.9	13.49
	SBI-06	42	sPbn-3837	28 - 50	4.43	15.8	-10.26
NSE (cd)	SBI-05	22	sPbn-0381	12 - 28	3.53	13.1	14.0
GYL (ww)	SBI-03	22	sPbn-5454	14 - 32	2.96	15.5	-1.79
	SBI-03	84	sPbn-7639	74 - 96	4.34	15.6	1.94
	SBI-04b	40	sPbn-0854	32 - 42	3.21	11.8	-2.04
	SBI-04b	58	sPbn-4420	48 - 58	3.45	12.9	2.26
	SBI-06	8	sPbn-7660	2 - 10	2.79	10.3	-1.53

Continued

GYL (cd)	SBI-04b	54	sPbn-4420	46 - 58	4.06	14.5	1.38
	SBI-06	8	sPbn-7660	2 - 10	2.94	10.5	-0.67
rel-GYL	SBI-05	8	sPbn-2880	6 - 16	3.87	15.6	0.14
PIN (ww)	SBI-02b	2	sPbn-2229	0 - 12	3.18	11.4	-2.02
	SBI-06	8	sPbn-7660	6 - 10	9.67	28.5	3.34
PIN (cd)	SBI-01	32	sPbn-4174	28 - 38	2.60	8.6	2.66
	SBI-01	46	sPbn-5684	40 - 54	3.13	10.3	-2.54
	SBI-06	14	sPbn-4036	10 - 20	10.71	31.0	3.51

^aTrait abbreviations are leaf area (LA), leaf dry weight (LDW), shoot dry weight (SDW), root dry weight (RDW), total dry weight (TDW), total root lengths (TRL), root to shoot ratio (RSR), specific leaf area (SLA), water use efficiency (WUE), panicle initiation (PIN), hundred kernel weight (HKW), number of seed per panicle (NSE) and grain yield (GYL). ^bLOD threshold for the experimental wise error rate $p < 0.05$.

Srinivas *et al.* (2009) [15] studied sorghum using 168 RILs derived from the cross of 296B × IS18551 and 152 genic-microsatellite markers. The study identified that one QTL GYL SBI-06 corresponds with the present study. Tuinstra *et al.* (1996) [13], using 98 RILs from the cross of B35 × Tx7078 and 150 RAPD plus 20 RFLP, detected four QTL on linkage group (LG) D and one QTL on LG H for GYL grown under pre-flowering drought conditions. One of the QTL on SBI-04 coincided with the present study. One interesting QTL region with QTL for NSE (cd), YLD (cd), LA (cd) and LDW (cd) on SBI-05 supports the hypothesis that high leaf area production under drought stress is directly related to increasing yields under stress.

5. Conclusion

We conclude from the present study that the main QTL regions controlling pre-flowering growth under drought stress conditions are located on chromosomes SBI-01, SBI-02 and SBI-06. Results support the hypothesis that genotypes considered to be drought tolerant may not outperform genotypes selected under non-stress conditions in most environmental scenarios, including stress situations [1] [31] [32]. We identified only one interesting QTL hotspot on SBI-05, in which QTL for yield and yield components were co-localized to QTL for vegetative plant growth under drought stress. However, further studies are needed to quantify drought stress effects during flowering and harvest time and to evaluate canopy development and yield formation of the present population under field conditions.

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