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DIVERSITY ARRAY TECHNOLOGY (DART) USED FOR MAPPING DROUGHT TOLERANCE IN COMMON BEAN

Boris Briñez[1], Alisson Fernando Chiorato[2], Sérgio Augusto Morais Carbonell[2], Luciana Lasry Benchimol-Reis[1]*

[1]*Centro de Pesquisa em Recursos Genéticos Vegetais, Instituto Agronômico (IAC), Campinas, SP, Brazil.*

[2]*Centro de Grãos e Fibras, Instituto Agronômico (IAC), Campinas, SP, Brazil.*

** Corresponding author: luciana.reis@sp.gov.br*

Abstract: Common bean (*Phaseolus vulgaris* L.) is an economically important crop principally in developing countries in Latin America, Africa and Asia. Drought is one of the main abiotic stresses worldwide and affects about 60% of the bean growing area. Advances in molecular marker technologies offer powerful methods to examine relationships between traits, generating a large volume of potentially useful information to help breeding programs. This study aimed to use the DArT (Diversity Arrays Technology) platform for common bean together with microsatellites (SSRs) and SNPs (Single Nucleotide Polymorphism) for mapping the AND 277 x SEA 5 population from CIAT (Colombia), and locating QTLs associated with drought tolerance. A total of 4,468 DArTs, 288 SNPs and 180 SSRs were used in genotyping. Phenotyping of the 105 inbred recombinant lines (RILs, F_8 generation) was performed by evaluating 18 traits associated with drought tolerance using a completely randomized design with four replications, applying a terminal stress in the vegetative phase V3/V4. Five SSRs, 91 SNPs and 4,468 DARTs were used for QTL detection which was performed through Statistical Machine Learning (SML). Eighteen QTLs were identified for the non-irrigated treatment for vase experiment and 05 QTLs for rhizotron experiment. All QTLs detected under drought conditions had the SEA 5 parent allele. This study is important for genetic improvement not only for a better understanding of the genetic inheritance of such a complex trait as drought tolerance, as well as for finding molecular tools to be used for marker-assisted selection.

Keywords: *Phaseolus vulgaris* L., water stress, molecular markers, SNPs, SSRs.

Introduction

The common bean is an annual legume domesticated more than seven million years ago, with two main centers of origin: Andean and Mesoamerican (Gepts and Bliss, 1984). Research around the world has been carried out to develop new cultivars that are more tolerant to periods of stress, more productive and resistant to diseases. It can be considered a plant sensitive to water stress, mainly due to its low recovery capacity after water deficit and poorly developed root system (Guimarães, 1992). It is estimated that drought affects 60% of the bean production area in the world (Wortmann et al., 1998; Beebe et al., 2010). There are important production areas such

as Mexico, Central America, southern Africa, and northeastern Brazil that receive less rainfall on average (Beebe et al., 2011). Plant response when subjected to water deficit is different depending on the drought pattern, which is especially variable in the tropics, where rainfall patterns can vary widely within a few kilometers (Beebe et al., 2012). Four drought patterns have been defined: late onset of rains; premature cessation of rains or terminal drought; intermittent drought, or little rain throughout the season (Fischer et al., 2003). Common bean genotypes show different reactions when exposed to water stress. Didonet and Silva (2004) reported that the common bean, when subjected to water stress, presents a reduction in leaf area and an increase in stomatal resistance. The reproductive phase is the most sensitive to water deficiency, with vulnerability from the beginning of flowering to the beginning of pod formation (Fageria et al., 1991), with the period from 5 to 10 days before anthesis being the most critical, which leads to a productivity reduction greater than 50% in yield (Norman et al., 1995).

Genetic knowledge as well as plant physiology makes it possible to associate genetic markers with specific responses to stress. Advances in molecular marker technologies offer powerful alternative methods for examining the relationships between these traits. Molecular markers have been widely used to study polymorphisms between DNA sequences such as microsatellites or SSRs (Simple Sequence Repeats, Tautz and Renz, 1984) and SNPs (Single Nucleotide Polymorphism, Gupta et al., 2001). SNP is one of the most common types of genetic variation existing in genomes, and because they are evolutionarily conserved, it has been used in studies to identify quantitative traits of interest such as drought tolerance (QTL – Quantitative trait *loci*; Briñez et al., 2017; Briñez et al, 2020).

The DArT technology ("Diversity Arrays Technology", Jaccoud et al., 2001) is based on hybridization on a platform that uses microarray technology for polymorphism analysis. It is a very efficient method in terms of cost/benefit ratio. A single DArT assay simultaneously genotypes hundreds to thousands of SNPs and INDELs across the genome of a species. The DArT procedure basically involves five steps: (1) construction of a genomic library (genomic representation); (2) printing of the genomic library on the microarrays; (3) labeling of genomic representations; (4) hybridization of the tagged genomic representation on the microarray followed by washes and (5) registration (by scanner) and data analysis. DArT comprises many advantages over other existing molecular markers: (1) DArT can perform analyzes in parallel rather than serially per marker data: many marker technologies are dependent on gel electrophoresis, resulting in poor performance. In polyacrylamide, between 50 to 150 fragments can be sampled at a time, while in an array high densities (+10,000) marker data can be obtained; (2) DArT does not require prior sequence information: many methods (SSRs, SNPs) require *a priori* sequence information. DArT is particularly interesting for species with few resources or no other technologies available; (3) DArT markers are genotyped with high efficiency: a specific software (DArTsoft) analyzes a large amount of data generated for each DArT experiment. The software analyzes the microarray images and subsequently identifies and genotypes the markers (Wenzl et al., 2004). The parameters of this program for quality are objectively established by the user who can select a set of markers with high quality and reproducibility; (4) DArT is an open platform: DArT Pty/Ltd. has established a network of DArT users (www.diversityarrays.com), to further develop and improve this technology; (5) The DArT platform allows application flexibility: the DArT libraries are prepared with individual or mixed genomes (for example: metagenomes) from individuals that best fit a desired application. For mapping studies, the parents of the segregating population are generally used, while for diversity studies the DNA can be derived from cultivated varieties and/or wild genotypes. The microarray platform is also flexible. In initial experiments, markers can be identified in the genomic library (discovery arrays). These markers can be rearranged on new slides (genotyping arrays) and serve for high-throughput detection of hundreds to thousands of markers in large populations.

The DArT technology has been shown to be efficient in studies of genetic diversity in germplasm collections, in addition to being suitable markers in molecular breeding programs (Kilian et al., 2005). The technology was developed for rice (Xie, 2006), cassava (Xia et al., 2005; Srisawada al., 2023), barley (Wenzl et al., 2004), wheat (Akbari et al., 2006, Semagn et al., 2006; Zeng et al., 2023), pigeon pea (Yang et al., 2006), eucalyptus (Grattapaglia et al., 2011), cowpea (Garcia-Oliveira et al., 2020), sorghum (Mace et al., 2008), banana (Risterucci et al., 2009) and Arabidopsis (Wittenberg et al., 2005). The technology has expanded to many other species including common bean (Briñez et al., 2012; Valdisser et al., 2017).

One of the advantages of the DArTs markers is that they can be sequenced immediately, which can be an advantage for the integration of genetic and physical maps through the anchoring of BACs, for example. This integration has already been successfully tested for Triticale (Alheit et al., 2011). In sugarcane, a crop that is difficult to genotype with other molecular markers due to different ploidies (allo, auto, aneuploid), with a high chromosome number (80 to 120), DArTs markers proved to be very suitable and with Mendelian inheritance (Aitken et al., 2014). The DArT platform was also suitable for BSA (Bulk Segregant Analysis) of quantitative traits in barley and wheat (Wenzl et al., 2007). In this last study, DArTs were used in wheat to perform BSA quantitatively, proving to be adequate and identifying *loci* associated with aluminum tolerance with an accuracy of less than 0.8 cM, regardless of the ploidy of the plants.

According to Wenzl et al. (2006), a consensus map for barley could be constructed by associating SSRs, RFLPs (Restriction Fragment Length Polymorphisms), STS (Sequence-tagged sites) and DArT markers, comprising 2,935 *loci*, of which 2,085 were from DArTs and 850 were from other markers. The map coverage was 1,161 cM. More than 98% of the map was covered by a single DArT trial. On average, 14 ± 9 DArT *loci* were identified within 5 cM on both sides of SSR, RFLP and STS precisely identified flanking regions linked to traits of agronomic interest.

Other maps have been constructed using DArT markers as described by Raman et al. (2012) where a linkage map was constructed for turnip (*Brassica napus* L.) by inserting 437 DArT, 135 SSR, and 6 gene markers with a total length of 2,288 cM. Petroli et al. (2012) established a map for eucalyptus with 2,274 DArT markers anchored to 210 SSRs. Lu et al. (2013) developed the DArT technology for tobacco and built a linkage map with 238 DArTs and 613 SSRs. Marone et al. (2012) studied the genetic and functional characteristics of DArT markers in wheat by analyzing sequences derived from DArT technology. Analyzes of the genetic positions of markers corresponding to almost identical sequences indicated that sequence redundancy is one of the factors that explain the agglomeration of these markers in specific regions of the genome. Furthermore, the authors concluded that the attribution of the function of putative genes makes these markers an ideal tool for synteny studies and/or for the identification of candidate genes.

DArT markers have been used in studies of diversity in germplasm banks (Yang et al., 2006), genetic mapping (Hippolyte et al., 2010) and gene identification (Grewal et al., 2008), and can be useful in marker-assisted selection (MAS), especially in monitoring the genome recovery of the recurrent parent (Varshney et al., 2010). The goals of this study was to: 1) Genotype 105 lines in the F_8 generation of the AND 277 x SEA 5 (AS) population using SSRs, SNPs and DArT markers; 2) Phenotypically evaluate the F_8 lines of the AS population regarding vases and roots in contrasting experiments, in irrigated and non-irrigated conditions; 3) Identify the number and chromosomal location as well as the type and magnitude of the effects of the QTLs involved in the response to water stress.

Material and Methods

Plant Material

The segregating population composed of 105 recombinant inbred lines (RILs) of common bean originated at CIAT (International Center

for Tropical Agriculture, Cali, Colombia) from the cross between the AND 277 cultivar and the SEA 5 cultivar. The F_8 generation was developed using the SSD (Single Seed Descent) method. Cultivar SEA 5 is an advanced CIAT line selected for drought tolerance, hence the designation SE A, from the "Advanced Drought" series, and it is considered a superior line from BAT 477 in terms of drought tolerance (Asfaw and Blair, 2011; Briñez et al., 2017). The drought tolerance of SEA 5 can be attributed mainly to the ability of this genotype to concentrate assimilates in grain production (Rao, 2001). The cultivar was derived from the initial cross (BAT 477 x San Cristobal) x (Guanajuato 31 x Rio Tibagi), has a type III indeterminate growth habit, small size and cream-colored seeds (Singh et al, 2001; Szilagyi et al, 2011). The cultivar AND 277 is based on the crossing of [Cargabello x (Pompadour Checa x Línea 17) x (Línea 17 x Red Kloud)] and presents the *Co*-1[4] allele and the *Phg*-1 gene that confer resistance to anthracnose (*Colletotrichum lindemuthianum*) and angular leaf spot (*Pseudocercospora griseola*), respectively (Gonçalves-Vidigal et al., 2011), but it is susceptible to drought. SEA 5 is of Mesoamerican origin and AND 277 of Andean origin.

Genotyping with SNPs and SSRs

Genotyping for the 384 SNPs was conducted using Vera Code® technology on the BeadXpress platform (Illumina) at the Biotechnology Laboratory of Embrapa Arroz e Feijão (Goiás, GO). A set of 384 SNP markers, validated through the Prelim file (*https://icom.illumina.com/Custom/UploadOpaPrelim/*), previously identified for *Phaseolus vulgaris* L. (Müller et al., 2015) and derived from the polymorphism between BAT477, of Mesoamerican origin, and Jalo EEP558, of Andean origin, were selected to compose the Oligo Pool Assay (OPA) of SNPs.

The SSRs used were derived from literature (Benchimol et al., 2007; Blair et al., 2003; Blair et al., 2006; Blair et al., 2008; Blair et al., 2009; Buso et al., 2006; Caixeta et al., 2005; Campos et al., 2007; Campos et al., 2011; Cardoso et al., 2008; Perseguini et al., 2011; Gaitán-Solís et al., 2002; Grisi et al., 2007; Guerra-Sanz, 2004; Hanai et al., 2007). The genotyping with SSRs and SNPs were performed as described in Briñez et al. (2017) and Briñez et al. (2020).

Phenotyping of plants

The phenotyping of plants grown in vases was described in Briñez et al. (2017) while the phenotyping of plants grown in rhizotrons for root evaluation was performed in Briñez et al. (2020).

Results and discussion

Map with DArT markers

The map constructed by the Diversity Arrays Technology company (www.diversityarrays), included 5 SSRs, 91 SNPs and 4,468 DArTs. The microsatellites were located on chromosomes Pv01, Pv07, Pv09 and Pv11. The SNPs were on the 11 chromosomes except for Pv10 and the DArTs were on all chromosomes with an average number of markers of 406 DArTs per chromosome, identifying the lowest saturation in the chromosome Pv05 with 269 markers, and the highest saturation on chromosome Pv07 with 555 markers (Table 1).

The map generated by the DArT Pty company (SSR-SNP-DArT, Table 1) showed greater saturation than the previous ones (SSR-SNP, Briñez et al., 2017 and Briñez et al., 2020) with many linked markers (4,468), a total length of 3,844.43 cM and saturation mean between markers of 0.79 cM. Only five microsatellites out of the 150 that were polymorphic in the parents, and 91 SNPs out of the 288 polymorphic in the population, were included. Population genotyping was performed using the "DArTseq" technology, which has the advantage of generating all sequences of markers inserted in the map for further analysis. However, the technology had several disadvantages in relation to the use of information with the use of available tools (softwares), mapping routines and map design, forcing the use of the company's "pipeline". When the map was built using the mapping software "OneMap" (Margarido

Table 1. Distribution of SSRs, SNPs and DArTs mapped on the 11 common bean chromosomes, in the genetic map developed by the DArT Pty company.

Chromosome	SSR	SNP	DART	No of Loci	Lenght (cM)	Distance between loci (cM)[1]
Pv01	1	16	489	506	322.95	0.77
Pv02	0	3	439	442	438.48	0.90
Pv03	0	13	395	408	513.15	0.85
Pv04	0	8	432	440	290.21	1.02
Pv05	0	8	261	269	311	0.8
Pv06	0	5	351	356	310.13	0.67
Pv07	1	10	544	555	335.88	0.77
Pv08	0	13	292	305	369.86	0.70
Pv09	2	9	399	410	377.14	0.81
Pv10	0	0	428	428	213.99	0.66
Pv11	1	6	438	445	361.64	0.78
Total	5	91	4,468	4,564	3,844.43	0.79

[1] Arithmetic mean

et al., 2007) and/or "Mapmaker" (Lander et al., 1987), inserting the DArTs, SSRs and SNPs, the DArT markers were linked in only three chromosomes, in the same position each, evidencing the presence of an artifact. When reducing the complexity, three different restriction enzymes were used (Briñez et al., 2012), one of which is of rare cutting, and two of frequent cutting that resulted in several sites scattered in the genome. When built with the company's "pipeline", most of the SSR markers were not linked to the map, indicating that there is a "gap" between the technologies for mapping these different types of markers.

Similar results were found by Jing et al. (2009) for wheat (*Triticum monococcum*) where DArTs and SSRs tended to form independent groups along the chromosomes. Several maps in other species have been built using these three types of markers in addition to the use of other markers such as AFLPs and RFLPs, with few SSRs being included in the map (Akbari et al., 2006). Wenzl et al. (2006) described the need to integrate the information generated by the DArT markers with the data produced from technologies based on the use of agarose and polyacrylamide gels. The authors describe that results with little reproducibility were found in the data set, with high density, analyzed using the JoinMap program (Stam, 1993). The difficulty of analyzing large amounts of data using this program was also found by other authors such as Isidore et al. (2003) and Van et al. (2005).

On average, each chromosome had more than 420 markers in each group, limiting the map design and exceeding the capacity of the program "Mapchart", software used for graphical presentation of linkage groups and QTLs (Voorrips et al., 2002). The Map presented a larger size than the maps mentioned above by other authors; however, the average distance between the markers was smaller than any other published maps, showing an advantage for its use in research genetic breeding programs, in addition to having all the sequences of the markers inserted in the SSR-SNP-DArT map.

Identification of QTLs in vases for the SSR-SNP-DArT map

Eighteen QTLs were identified in the non-irrigated treatment by the DArT Pty company using the company's own "pipeline". QTLs for chlorophyll, leaf area, stem fresh mass, leaf dry mass, stem dry mass, leaf temperature, number of seeds per pod, mass of 100 seeds and days to flowering were detected. The most effective QTLs were for chlorophyll (C6.2AS), leaf area (LA3.1AS), stem fresh weight (SBF3.1AS), number of seeds per pod (NSP10.1AS, NSP 1.1AS, NSP5.1AS) and mass of 100 seeds (SW1.1AS) (Table 2).

Table 2. Description of the QTLs identified in the experiment in vases in the non-irrigated treatment related to drought tolerance found via Statistical Machine Learning (SML) analysis, using the common bean AS (AND 277 × SEA 5) genetic map with the SSR-SNP-DArT markers. The identified QTLs were named according to the characteristic of the QTL found in the experiment with non-irrigated vases. The peak marker of the graphs of each QTL, in their respective chromosomes, the PAVE or level of significance and the position of each QTL in cM are also presented.

Trait	Chr	QTL	Marker	Pave	Position (cM)
Chlorophyll	Pv06	C6.2^{AS}	100025029|F|0	0.051	106.78
Chlorophyll	Pv06	C6.2^{AS}	100018482|F|0	0.026	106.78
Foliar Area	Pv03	LA3.1^{AS}	100015192|F|0	0.022	118.78
Foliar Area	Pv03	LA3.2^{AS}	100027180|F|0	0.010	122.63
Fresh stem mass	Pv03	SBF3.1^{AS}	100004453|F|0	0.021	289.49
Fresh stem mass	Pv03	SBF3.2^{AS}	100028860|F|0	0.018	250.65
Leaf dry mass	Pv08	LBD8.1^{AS}	BARC-PV-0004144	0.016	212.86
Leaf dry mass	Pv08	LBD8.2^{AS}	BARC-PV-0002954	0.011	210.48
Stem dry mass	Pv02	SBD2.1^{AS}	100027898|F|0	0.012	12.62
Leaf temperature	Pv08	LT8.1^{AS}	100010997|F|0	0.011	50.94
N°Seeds/pod	Pv10	NSP10.1^{AS}	100041132|F|0	0.028	68.16
N°Seeds/pod	Pv01	NSP1.1^{AS}	100035462|F|0	0.021	295.46
N°Seeds/pod	Pv05	NSP5.1^{AS}	100022390|F|0	0.021	150.97
N°Seeds/pod	Pv04	NSP4.1^{AS}	100043301|F|0	0.011	215.95
N°Seeds/pod	Pv01	NSP1.1^{AS}	100030921|F|0	0.010	217.88
Seed mass (g/100s)	Pv01	SW1.2^{AS}	100008797|F|0	0.064	38.08
Days until flowering	Pv05	DF5.1^{AS}	100030163|F|0	0.016	6.00
Days until flowering	Pv01	DF1.1^{AS}	100016108|F|0	0.014	205.65

Chr= Chromosome; PAVE: statistically significant ≥ 0.1

Bedo et al. (2008) compared the performance of SML (Statistical Machine Learning), CIM (Composite Interval Mapping), BIM (Bayesian Interval Mapping) and MR (Single Marker Regression) methodologies in a dataset of a progeny from a cross between two cultivars of barley. The results showed that the SML method accurately identified the QTLs while the BIM method underestimated the number of QTLs. The QTLs identified by SML coincided with the location of those known in the literature. The SML methodology evidenced approximately half of the QTLs reported by the CIM and MR analyses, which is expected since these latter methodologies do not use independent tests. These last two methods were also likely to produce optimistic estimates of QTL effects. The QTL resolution (peak definition) offered by the SML was consistently superior to the MR, CIM and BIM methods. The authors concluded that the SML methodology produces better estimates of the QTLs´ effects because it eliminates the optimistic bias in the predictive performance of the other QTL identification methods, in addition to producing narrower peaks than the other methods, except for the BIM method, and therefore, identifies QTLs more accurately. It is more robust for genotyping and linkage mapping and identifies markers linked to QTLs in the absence of a genetic map.

Identification of QTLs in rhizotron from the SSR-SNP-DArT map

Ten QTLs were identified by the DArT Pty company for the irrigated treatment for the characteristics chlorophyll, leaf area, leaf fresh mass, stem fresh mass, leaf dry mass, root length, root surface area and leaf temperature being the highest effect for leaf area (LA1.1AS), stem fresh mass (SBF3.1AS), leaf dry mass (LBD 1.1AS), root length (RL1.1AS) and root surface area (RSA10.1AS) (Table 3).

Table 3. Identification of QTLs in the rhizotron experiment with the AS (AND 277 x SEA 5) population in the irrigated treatment found via SML (Statistical Machine Learning) analysis from the map with the SSR-SNP-DArT markers. The peak marker of each QTL, in their respective chromosomes, the PAVE or level of significance and the position of each QTL in cM are also presented.

Trait	QTL	Chr	Marker	PAVE	Position (cM)
Chlorophyll	C9.1^{AS}	Pv09	100025821	0.013	325.12
Foliar area	LA1.1^{AS}	Pv01	100032102	0.022	213.14
Fresh leaf mass	LBF1.1^{AS}	Pv01	100032102	0.011	213.14
Fresh stem mass	SBF3.1^{AS}	Pv03	100016086	0.020	390.68
Fresh stem mass	SBF6.1^{AS}	Pv06	100089317	0.011	261.69
Dry leaf mass	LBD1.1^{AS}	Pv01	100024096	0.023	213.14
Dry leaf mass	LBD1.2^{AS}	Pv01	100030811	0.016	233.34
Root length	RL1.1^{AS}	Pv01	100009123	0.020	202.03
Root surface area	RSA10.1^{AS}	Pv10	100021789	0.023	80.35
Leaf temperature	LT1.1^{AS}	Pv01	100013136	0.013	213.14
Leaf temperature	LT9.1^{AS}	Pv09	100015358	0.011	156.38

Chr=Chromosome; PAVE: statistically significant ≥ 0.1

For the non-irrigated treatment, five QTLs were identified, three for leaf area, one for stem fresh mass and another for root volume. The QTL with the greatest effect was for leaf area (LA8.1AS) on chromosome Pv8 (Table 4).

Table 4. Identification of QTLs in the rhizotron experiment with AS (AND 277 x SEA 5) population in the non-irrigated treatment found via SML (Statistical Machine Learning) analysis from the map with the SSR-SNP-DArT markers. The peak marker of each QTL, in their respective chromosomes, the PAVE or level of significance and the position of each QTL in cM are also presented.

Trait	QTL	Chr	Marker	PAVE	Position (cM)
Leaf area	LA8.1^{AS}	Pv08	100023528	0.03	309.76
Leaf area	LA3.1^{AS}	Pv03	100006334	0.01	454.45
Leaf area	LA2.1^{AS}	Pv02	100018180	0.01	31.24
Fresh stem mass	SBF8.1^{AS}	Pv08	100015514	0.01	326.24
Root Volume	RV2.1^{AS}	Pv02	100088280	0.01	401.25

Chr=Chromosome; PAVE: statistically significant ≥ 0.1

Phenotypic selection for root traits is a slow and laborious process, which justifies the search for alternative strategies, such as the identification of QTLs in greenhouses followed by indirect selection using highly reproducible markers. The association of root characteristics and genetic markers through a QTL mapping approach in a stable population of RILs evaluated in experiments with replications and duly conducted, can contribute to a better understanding of the variability of the hereditary characteristics of interest for the root (Asfaw and Blair, 2012). This approach has been used in genetic control studies for root traits in improving drought tolerance in rice (*Oryza sativa*; Steele et al., 2006; Courtosis et al., 2009), maize (*Zea mays*; Tuberosa et al., 2007; Ruta et al., 2010) and chickpeas (*Cicer arietinum*; Vadez et al., 2008; Gaur et al., 2008).

In common bean, QTL analyzes have been used in the analysis of root hairs and rhizosphere acidification (Yan et al., 2004), basal root development and adaptation to low phosphorus levels (Ochoa et al., 2006), root response to auxins (Remans et al., 2008). The identification of common bean root QTLs with an effect on drought tolerance was reported by Asfaw and Blair (2012), in which QTLs were detected for root dry mass, volume, and root length. These QTLs were identified in Pv11 unlike the QTLs revealed in this study that were localized for root volume on chromosome Pv02 in the non-irrigated treatment.

With the aim of validating the QTLs identified in this study and estimating their stability, future experiments in the field evaluating different years and locations should be carried out before their application in genetic improvement programs as an indirect method of selection. Studies that allow markers to be linked to specific alleles that co-segregate with tolerance *loci* were identified, enabling the positional cloning of tolerance genes. Stable QTLs were detected, so that the region of these QTLs can be refined to be used for marker-assisted selection.

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