



GGE biplot and QTL analyses for seed yield in an Andean population of common bean

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Abstract Seed yield of common bean (*Phaseolus vulgaris* L.) is genetically complex. The objectives of this study were to: i) evaluate the four testing environments of the University of Zambia (UNZA) Bean Breeding program using Genotype plus Genotype by Environment biplot analysis, ii) identify the best performing genotype in all four testing environments, and iii) map the quantitative trait loci (QTL) for seed yield in an Andean population of recombinant inbred lines. A total of 155 F₁₀ recombinant inbred lines were evaluated for seed yield in seven field trials conducted in four testing environments namely Golden Valley Agricultural Research Trust (GART), UNZA, Kabwe and Mpika located in Zambia. All four testing environments were located in a single mega-environment, and the RIL SA135 being the best performer in this mega-environment. The population was genotyped with 5,398 single nucleotide polymorphism markers, and QTL analysis was conducted. A total of

four QTL for seed yield specific to the testing environments GART and Mpika were mapped on chromosomes Pv02, Pv04, Pv06 and Pv09. The amount of variation in seed yield explained by individual QTL ranged from 6.0 to 8.2%. The QTL YLD2.1^{SA} and YLD4.1^{SA} overlapped with previously identified seed yield QTLs.

Keywords Common bean · GGE · QTL · Recombinant inbred line · Yield

Introduction

Common bean (*Phaseolus vulgaris* L.) is the most important legume for direct human consumption (Broughton et al. 2003; Uebersax et al. 2023). It is a major source of income, calories, protein and essential micronutrients (iron and zinc) for many households in Africa and Latin America (Uebersax et al. 2023). Despite its economic and nutritional importance, common bean yields remain low particularly in Africa. Common bean global production and average yield is estimated at 27.5 million metric tons and 715 kg/ha, respectively (Uebersax et al. 2023). Average seed yield for Africa is less than 1 t ha⁻¹ (Katungi et al. 2009; Farrow and Muthoni-Andriatsitohaina 2020). In Zambia, which has an estimated common bean annual production of about 65 000 MT, and a net importer, the average yield is about 750 kg ha⁻¹, which is similar to most African countries but lower

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than average yields in North America (Uebersax et al. 2023).

Seed yield is the most important agronomic trait; therefore, its genetic enhancement is invariably a breeding objective for any breeding program. However, breeding for increased seed yield remains challenging because of its genetic complexity (Kelly et al. 1998). Several genes with small additive effects control seed yield. These genes significantly interact with the environment resulting in low to moderate heritability and small genetic gains for seed yield (Nienhuis et al. 1988; Hoyos-Villegas et al. 2015; Mutari et al. 2022; Ramírez-Vallejo and Kelly 1998; Schneider et al. 1997). Breeders have extensively used Genotype plus Genotype by Environment (GGE) biplot analysis for genotype and mega-environment analysis (Yan et al. 2000; Hoyos-Villegas et al. 2016a). Biplots provide important insights into the discriminativeness and representativeness of the testing sites, which is important to making decisions in a breeding program on the optimum number of testing sites needed given the resource constraints encountered by breeding programs especially public breeding programs. The “which-won-where” view on the biplot has been used to subdivide the target regions or group testing locations into mega-environment (Yan and Hunt 2001; Yan and Tinker 2006).

Identification and use of molecular markers linked to major-effect quantitative trait loci (QTL) controlling yield could potentially contribute to development and use of genomic approaches to circumvent the challenges of directly selecting for yield. To-date several quantitative trait loci (QTL) for seed yield have been identified on all eleven chromosomes of common bean. The majority of these identified QTLs explain less than 10% of variation in seed yield in their respective populations. Application of QTL analysis results for seed yield in marker-assisted selection remains limited due to various reasons including lack of stability of the identified QTL in different environments and genetic backgrounds. There are, however, few seed yield QTL that are stable across environments and genetic backgrounds. For example, six independent studies have consistently reported seed yield QTL on the genomic region 33 Mbp – 39 Mbp on chromosome Pv03 using diverse populations evaluated in diverse environments (Mukeshimana et al. 2014; Kamfwa et al. 2015;

Hoyos-Villegas et al. 2015; Farid 2015; Hoyos-Villegas et al. 2016b; Helig et al. 2017; Hamabwe et al. 2023). Co-localization of several seed yield QTL on this genomic region provides encouraging prospects of potential use of QTL information in Marker-assisted selection for seed yield. The objectives of this study were to: i) evaluate the four testing environments of the University of Zambia (UNZA) Bean Breeding program using Genotype plus Genotype by Environment (GGE) biplot analysis, ii) identify the best performing genotype in all four testing environments, and iii) map the quantitative trait loci (QTL) for seed yield in an Andean population of recombinant inbred lines.

Materials and methods

Plant materials

In this study, a population of 155 F₁₀ Recombinant Inbred Lines (RILs) derived from Solwezi and AO-1012–29-3-3A (AO-3A) were evaluated for seed yield in seven field experiments. Solwezi is an Andean Zambian landrace with an indeterminate growth habit (Type III). AO-3A is a determinate, Andean variety developed co-operatively by Sokoine University, University of Puerto Rico, Oregon State University and USDA-ARS. AO-3A is resistant to seed weevils (*Acanthoscelides obtectus*) and bean common mosaic virus (Kusolwa et al. 2016; Kamfwa et al. 2018). Additionally, AO-3A is resistant to some races of *Colletotrichum lindemuthianum* the causative pathogen of anthracnose (Mungalu et al. 2020). The RILs were developed using the single seed descent method.

Field trials

The 155 RILs and their parents were evaluated for seed yield in seven field trials conducted at four locations including University of Zambia research farm, Golden Valley Research Trust, Kabwe Agricultural Research Station and Mpika Agricultural Research Station in 2017, 2018, 2019, 2020 and 2021 growing seasons. All seven

trials were conducted during the rainy season (with no irrigation) using a randomized complete block design. For each of the seven trials three replications were used and an experimental plot was comprised of two rows that were 4 m long with an inter-row spacing of 0.6 m.

Field trials at University of Zambia Research farm, Lusaka, were conducted in the years 2017 and 2019, here after referred to as UNZA_17 and UNZA_19, respectively. University of Zambia research farm is located in agro-ecological zone II (coordinates: -15.39, 28.31), which has an annual rainfall of 800 mm–1000 mm. The soil for the trial site University of Zambia Research Farm is classified as fine loamy isohyperthermic paleustalf.

Field trials at Mpika Research Station were conducted in the years 2018, 2020 and 2021, here after referred to as Mpika_18, Mpika_2020 and Mpika_2021, respectively. Mpika Research Station is located in region III (coordinates: -11.80, 31.45) and receives annual rainfall of 1200 mm. The soil at this station is classified as red soil.

Golden Valley Agricultural Research Trust (GART) is in agro-ecological zone II (coordinates: -14.97, 28.09), and only one field trial was conducted, and this was in 2021 (here after referred to as GART_2021). The soil at GART is classified as fine, mixed isohyperthermic udic paleustoll. Also, only a single field trial was conducted at Kabwe Research Station in 2021 (here after referred to as Kabwe_2021). The soils at Kabwe are classified as sandy loam soils. Both GART and Kabwe Research Station are in agro-ecological zone II with an annual rainfall of 800 mm – 1000 mm.

For all seven trials, the fertilizer “D-compound” (10 Nitrogen: 20 Phosphorus: 10 Potassium: 6 Sulfur) was applied at a rate of 200 kg ha⁻¹ at planting. Each trial was hand-weeded three times to ensure the crop was weed-free. The crop was hand- harvested and the grain dried in the drier at 50 °C for 72 h to standardize the grain moisture content. Seed yield was initially measured on a plot basis and then final yield mean yield for each genotype was adjusted to kg ha⁻¹.

Genotype plus genotype by environment (GGE) biplot analysis

A linear mixed model was used to determine variation resulting from genotype (G), environment (G)

and genotype-by-environment (GE) interactions. The package ASReml-R (Butler 2017) was used to create a mixed-effect model and solve for the best linear unbiased predictors (BLUPs). The BLUPs for each genotype in each location were used to generate GGE biplots with the *metan* package in R (Olivoto 2020).

Genotyping and QTL analysis

DNA was extracted using the CTAB method from RILs and their parents from seedlings grown in the greenhouse at Michigan State University. The population was then genotyped using the Illumina BARC-Bean6K_3 BeadChip with 5,398 SNPs (Song et al. 2015) in the Soybean Genomics and Improvement USDA Laboratory (USDA-ARS, Beltsville Agricultural Research Center) in MD, USA. Of the 5398 SNPs, 760 SNPs were polymorphic between parents and were used to build a linkage map using JoinMap version 4.1 (Van Ooijen 2011). A total of 11 linkage groups corresponding to the 11 bean chromosomes were built. The number of markers per linkage group ranged from 16 (chromosome Pv01) to 84 (chromosome Pv04) with an average size of 47 SNPs per linkage group. The linkage group size ranged from 41.4 cM (chromosome Pv06) to 83.6 cM with an average size of 55.8 cM.

The BLUPs for each genotype in each location and across the four locations were used to map the QTL using composite interval mapping (CIM) in the software Win QTL Cartographer version 2.5–011 (Wang et al. 2012). The following parameters were used for CIM: (i) model 6 (Standard model), (ii) five control/background markers, (iii) 10 cM window size, and (iv) forward and backward multiple regression model, (v) 1 cM walk speed (genome scan interval). A permutation test (1000 permutations) was used to determine the LOD threshold of 3.0, which was used to determine the statistical significance of the QTL. The software Mapchart (Voorrips 2002) was used to display the linkage maps with QTL on them. The coefficient of determination (R^2) was used to estimate the proportion of variation in yield explained by a QTL.

Table 1 Means and ranges for seed yield measured on parents (Solwezi and AO-1012-3-3A) and 155 recombinant inbred lines grown in Zambia in the field at University of Zambia

(UNZA) research farm, golden valley agricultural research trust (GART), Kabwe, and Mpika in 2017, 2018, 2019, 2020 and 2021

Trial name	Parents			RILs (155)		
	A0 (kg)	SZ (kg)	<i>t</i> -test	Mean (kg)	Range (kg)	ANOVA
UNZA_17	837	1,300	**	1,261	84–3,185	**
UNZA_19	579	748	**	752	92–2,546	**
MPIKA_18	775	362	**	718	114–2,988	**
MPIKA_20	408	785	**	530	79–1,712	**
MPIKA_21	818	937	**	943	147–2,586	**
KABWE	802	916	*	798	166–1,926	**
GART	479	1,225	**	954	132–2,551	**

RILs=recombinant inbred lines; \pm S.E the Mean; *t*-test represent the level of significance for the *p*-value of a *t*-test between parental means; ANOVA=Analysis of Variance; * =0.05 (level of significance); ** =0.01 (level of significance); AO=AO-1012-29-3-3A; SZ=Solwezi

Results

Seed yield

There were significant ($p < 0.05$) differences among RILs for yield in all seven field trials. The average yields for trials ranged from 530 kg ha⁻¹ (Mpika_20) to 1,261 kg ha⁻¹ (UNZA_17) (Table 1). The highest yield (3,185 kg ha⁻¹) for a RIL across the seven trials was recorded from the trial UNZA_17. The *t*-test results showed significant yield differences between Solwezi and AO-3A (Table 1). The parent Solwezi had higher seed yield than AO-3A in all seven trials except Mpika_18 where AO-3A had higher yield than Solwezi.

Evaluation of the testing environment

GGE biplot analysis was conducted to evaluate the four testing environments (discriminateness and representativeness) and identify the best performing genotypes in the testing environments (which-won-where). Principal components 1 and 2, which explained 44.9% and 26.7% of seed yield variation, respectively, were used to develop the GGE biplots. A plot of environment vectors indicated strong correlations among the four testing environments as the angle between the vectors of the two furthest sites GART and Mpika was acute (≤ 90 degrees) (Fig. 1).

GART and Kabwe were the most discriminating environments, while UNZA and Mpika were less

discriminating (Fig. 2). Ranking of the four environments relative to the ideal based on the discriminativeness and representativeness showed that all four testing sites were away from the ideal environment (Fig. 3).

The equality lines on the polygon divided the biplot into several sectors. All four testing environments were in the same sector indicating that these four testing environments form a single mega-environment. The best performing genotype in this mega-environment was SA135 (Fig. 4).

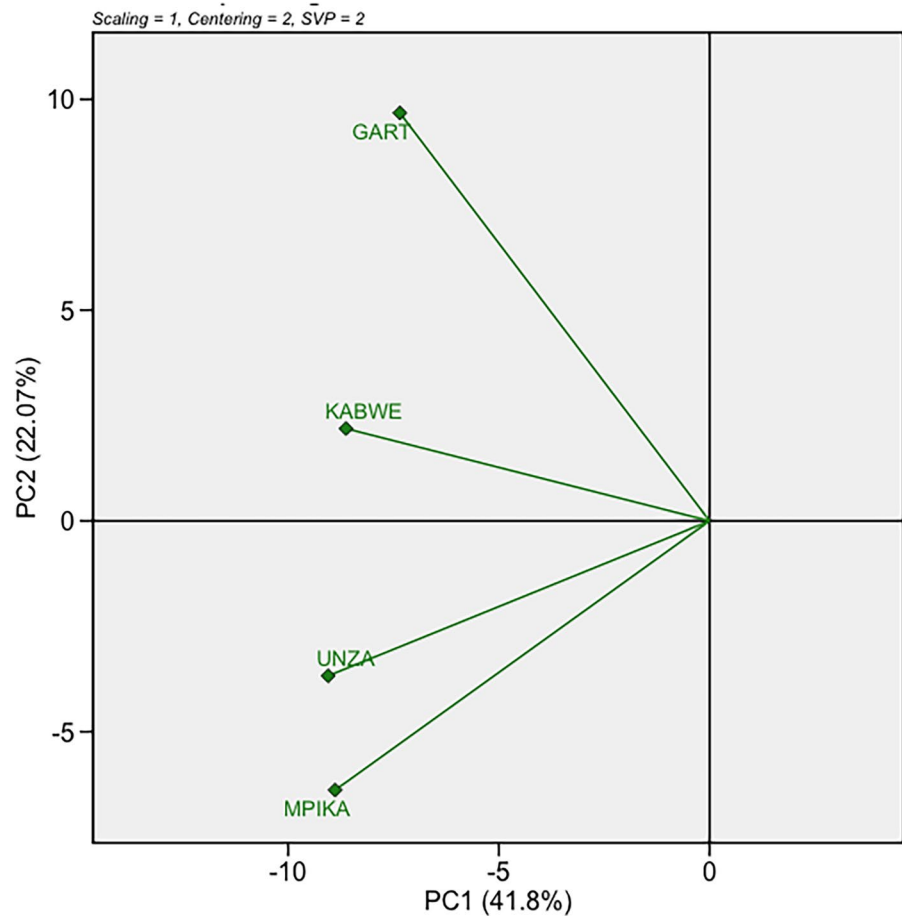
QTL analysis

A total of four QTLs on chromosomes Pv02, Pv04 and Pv09 were detected in the current study (Table 2 and Fig. 5). QTL positions of from the current study are reported in physical distances, for easy comparison with previously reported QTL.

The QTL YLD2.1^{SA}, which was mapped at 45.4–46.5 Mbp of Pv02 was detected from GART. The R^2 for this QTL was 8.2%, and the parent Solwezi contributed the positive allele at this QTL.

QTL YLD4.1^{SA} was mapped at 43.8–45.3 Mbp of chromosome Pv04 with a R^2 of 7.3% and the parent Solwezi contributed the positive allele. This QTL was also detected from Mpika trial. A second QTL YLD4.2^{SA} was mapped to 3.2–4.1 Mbp of Pv04. This QTL explained 7.4% of seed yield variation at GART, and Solwezi contributed the positive allele. YLD9.1^{SA} was mapped to 15.2–16.2

Fig. 1 Relationships among four testing environments i.e., University of Zambia (UNZA), Golden Valley Agricultural Research Trust (GART), Kabwe and Mpika



Mbp of Pv09. The R^2 for this QTL was 6.0% and Solwezi contributed the positive allele.

The additive yields advantage provided by the four QTLs identified in the current study ranged from 142 to 167 kg ha⁻¹ (Table 2).

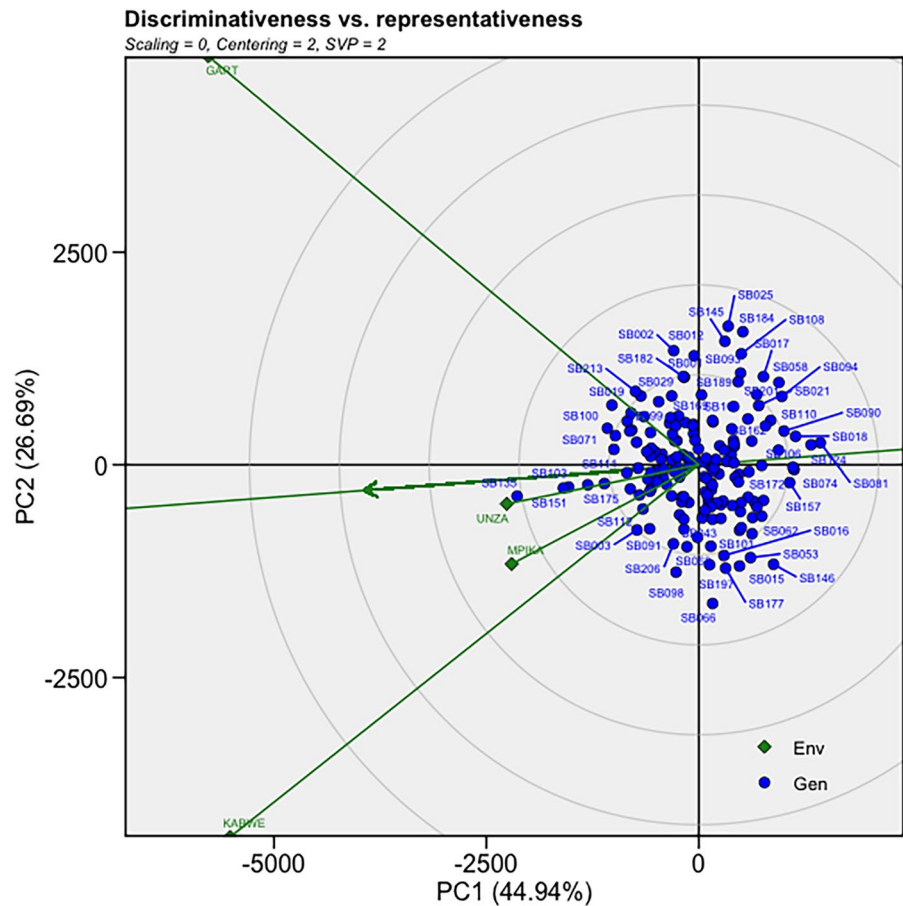
A multiple QTL model analysis for the three QTL identified in GART on Pv02, Pv04 and Pv09, revealed that these three QTL accounted for a total of 21.9% of the variation in seed yield at GART.

Discussion

GGE biplot analysis from this study provided useful information on the four testing environments for the UNZA Bean Breeding program. The two testing sites Mpika and UNZA were highly correlated suggesting that both sites provided similar seed yield information. This suggests that one of these two environments

can be dropped as a testing site to make savings in the testing costs for the UNZA Bean Breeding program. The preference would be to maintain Mpika because it is located in a major bean-producing area and experiences higher anthracnose pressure than UNZA (Sansala et al. 2023). Anthracnose is a major disease in Zambia. This higher anthracnose pressure that Mpika normally experiences would be important for selection for anthracnose resistance under field conditions. Among the four testing sites Mpika and UNZA were the least discriminating, and these two sites should be given less priority for testing of breeding materials because they are less informative. Given that all four environments fell in one mega-environment, genotypes that can be tested in the more discriminating environments such as Kabwe or GART can be deployed in the entire mega-environment including Mpika and UNZA, which are the two locations that may not be suitable for selection given their

Fig. 2 Discriminativeness versus representativeness among four testing environments i.e., University of Zambia (UNZA), Golden Valley Agricultural Research Trust (GART), Kabwe and Mpika



lack of discriminativeness. The genotype SA135 was identified as best performing genotype in the identified mega-environment, and this genotype can be considered for release as a variety in Zambia given that it is in a market class acceptable to Zambian consumers.

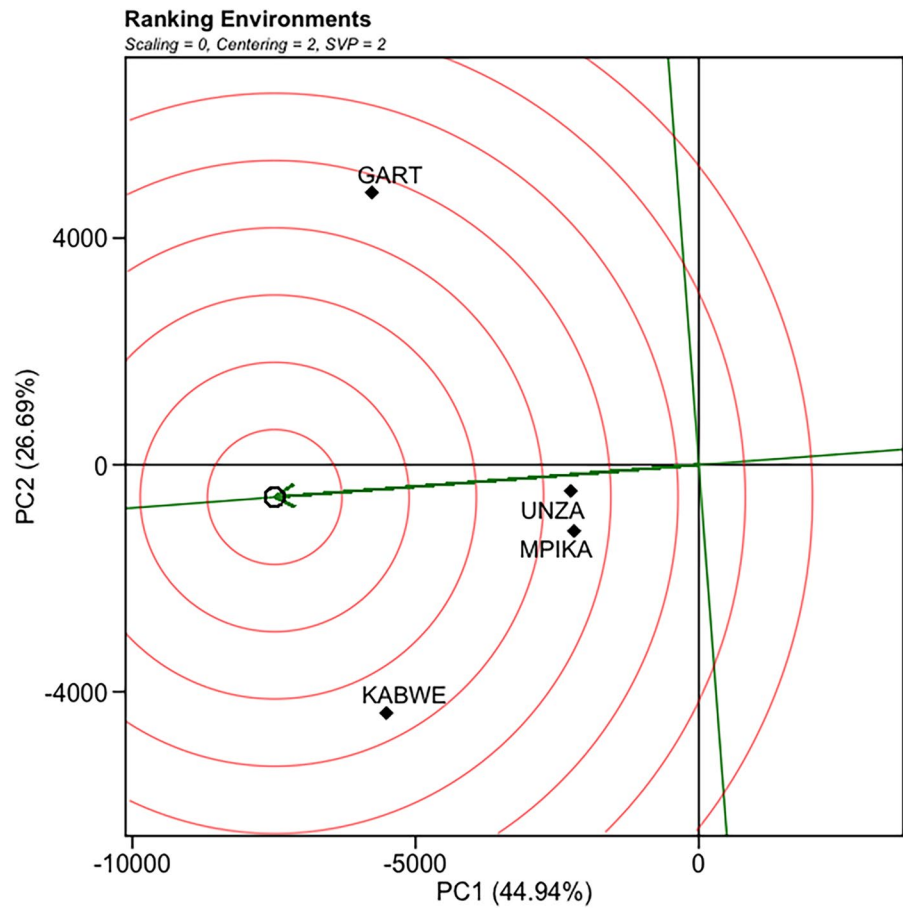
In the current study a total of four QTL for seed yield were identified (Table 2). All four QTLs were specific to the testing environment GART and Mpika. Both parents Solwezi and AO-3A contributed positive alleles at the identified QTL in the current study, which provided evidence for the presence of positive seed yield alleles even in the parent AO-3A, which had lower yield in six of the seven trials conducted in the current study. The contribution of positive alleles from both parents provides further evidence to the genetic basis of transgressive segregation observed in all seven trials in the current study (Table 1).

YLD2.1^{SA} was detected on Pv02 (45.4–46.5 Mbp) from GART. This QTL overlapped with previously

reported QTL for seed yield in the Andean gene pool (Keller et al. 2020).

Two QTL (YLD4.1^{SA} and YLD4.2^{SA}) were identified on Pv02. YLD4.1^{SA} was identified in Mpika trials. YLD4.1^{SA} was mapped to a genomic region 43.8 Mbp–45.3 Mbp, which overlapped with previously identified seed yield QTL in two genome-wide association studies that used Andean and Middle American diversity panels grown under drought stress condition (Dramadri et al. 2021; Mutari et al. 2023). Additionally, YLD4.1^{SA} overlapped with previously identified seed yield QTL from a Middle American population derived from ICA Bunsu and SXB405 (Berny Mier y Teran et al. 2019). This overlap of YLD4.1^{SA} with previous QTL in both Andean and Middle American gene pools suggests that it is stable across genetic

Fig. 3 Ranking of four testing environments i.e., University of Zambia (UNZA), Golden Valley Agricultural Research Trust (GART), Kabwe and Mpika



backgrounds and environments. YLD4.2^{SA}, which was only identified in GART did not overlap with any previously identified QTL.

All four QTLs reported in this study had relatively low R^2 values (6.0–8.2), which were consistent with previously reported estimates and genetic complexity of seed yield, which involves mostly minor-effect QTL with additive action (Kamfwa et al. 2015; Hamabwe et al. 2023). The total R^2 value for the three QTL identified in GART was 21.9%, suggesting that a significant portion of seed yield variability at GART could not be explained just by the three identified QTL. It is plausible that the unexplained variation could have been caused by minor-effect QTL which we could not identify in our analysis.

Conclusion

All four testing environments were strongly correlated, provided similar yield information and were plotted in a single mega-environment. The RIL SA135 was the best performer in this mega-environment. Four seed yield QTL specific to testing sites GART and Mpika were detected on Pv02, Pv04 and Pv09. The QTL YLD2.1^{SA} and YLD4.1^{SA} overlapped with previously reported QTL while the other two did not.

Fig. 4 The which-won-where view of the GGE biplot

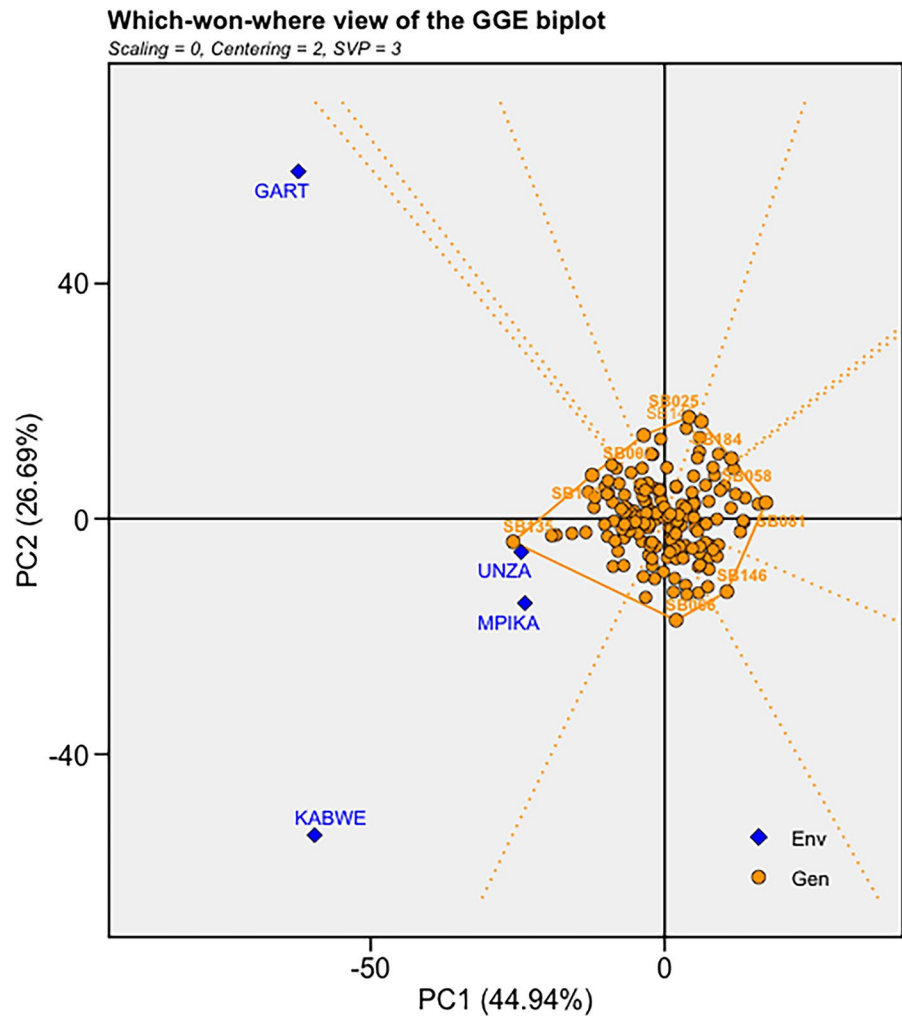


Table 2 Quantitative trait loci for seed yield identified in a population of 155 recombinant inbred lines derived from a Solwezi x AO-1012–29-3-3A grown in Zambia in the field at

University of Zambia (UNZA) Research Farm, Golden Valley Agricultural Research Trust (GART), Kabwe, and Mpika in 2017, 2018, 2019, 2020 and 2021

Location	QTL Name	CHR	Peak nearest SNP [Position (Mbp)]	QTL Interval (Mbp)	LOD	R^2	Add	Source
GART	YLD2.1 ^{SA}	Pv02	ss715646163 (45.8)	45.4–46.5	3.7	8.2	167	SZ
Mpika	YLD4.1 ^{SA}	Pv04	ss715645798 (43.8)	43.8–45.3	3.0	7.3	142	SZ
GART	YLD4.2 ^{SA}	Pv04	ss715648124 (4.1)	3.2–4.1	3.4	7.4	162	SZ
GART	YLD9.1 ^{SA}	Pv09	ss715648557 (15.2)	15.2–16.2	3.0	6.0	147	SZ

The superscript SA=Solwezi x AO-1012–29-3-3A; Mb=Million base pairs; LOD=logarithm of odds; CHR=Chromosome; R^2 =proportion of phenotypic variance explained by the QTL; Add=Additive effects of the QTL; AO=AO-1012–29-3-3A; SZ=Solwezi

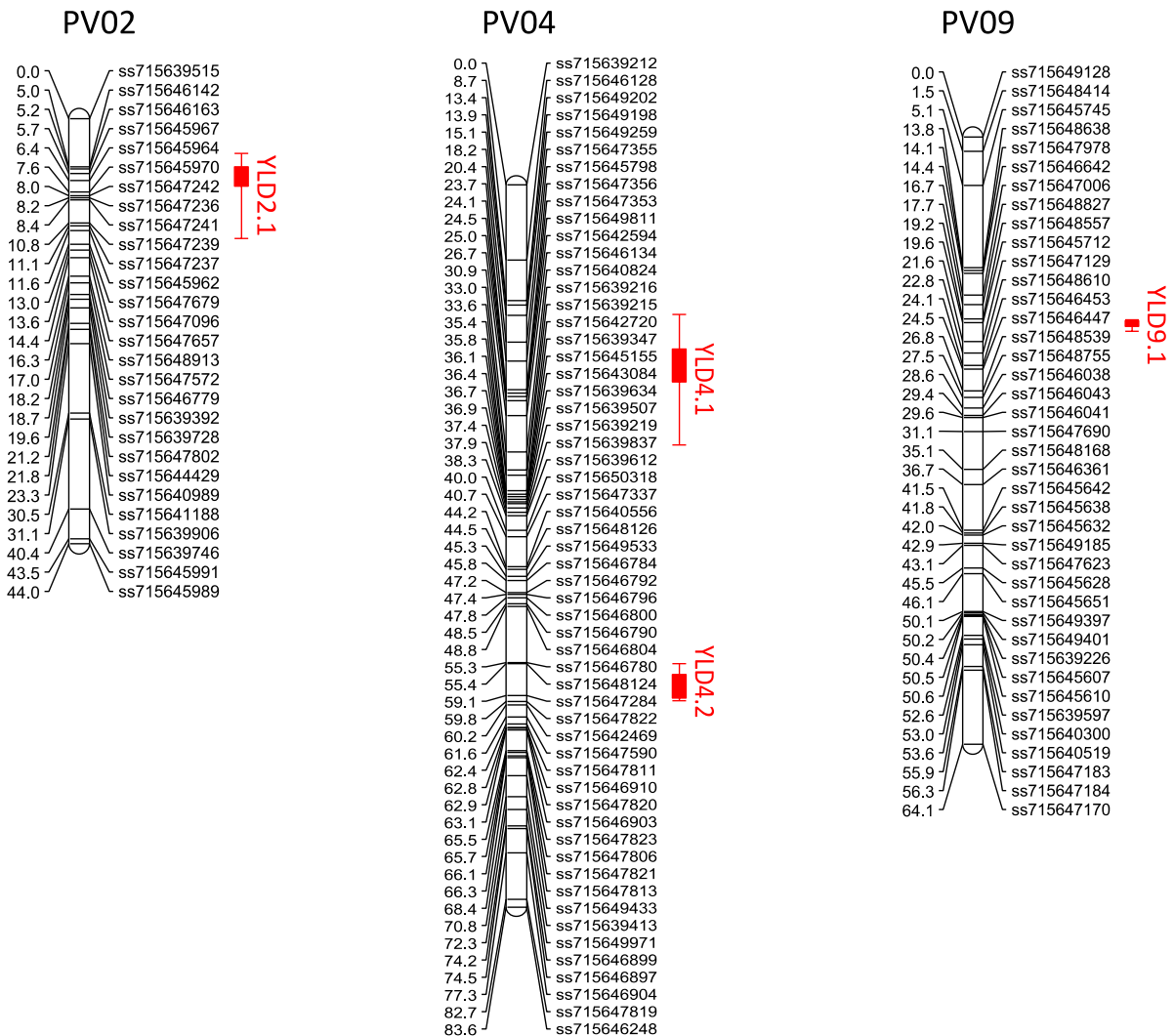


Fig. 5 Linkage maps with identified quantitative trait loci for seed yield on chromosomes Pv02, Pv04 and Pv09 in a Solwezi x AO-1012–29-3-3A mapping population

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Author contributions SS conducted the experiments, data analysis, interpretation and drafted the manuscript. SH conducted the experiments and edited the manuscript. BM conducted the experiments and edited the manuscript. KK conducted the experiments and edited the manuscript. DL interpreted results and edited the manuscript. IC conducted data analysis, interpreted results and edited the manuscript. VV conducted data analysis, interpreted results and edited the manuscript. KK conducted the experiments, data analysis, interpreted results and drafted the manuscript. All authors read and approved the final manuscript.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare no competing interests.

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