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RESEARCH ARTICLE

Phenotypic characterisation and genetic dissection of the yield-attributing traits of exotic quinoa (*Chenopodium quinoa* L.) germplasm

Sadia Akter[1], Biswajit Das[1], Adrita Abdullah[1], Fauzia Afrin Aurin[1], Naima Sultana[1], Md Moshiur Rahman[2], David J. Burritt[3] & Mohammad Anwar Hossain[1*]

[1]Department of Genetics and Plant Breeding, Bangladesh Agricultural University, Mymensingh 2202, Bangladesh
[2]Department of Agronomy, Bangladesh Agricultural University, Mymensingh 2202, Bangladesh
[3]Department of Botany, University of Otago, Dunedin 9016, New Zealand

*Correspondence email - anwargpb@bau.edu.bd

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Abstract

Quinoa (*Chenopodium quinoa* L.) is a highly nutritious, climate-resilient crop with high levels of phenotypic and genotypic variability. Three replications of a randomised complete block design (RBCD) were used in a field experiment at the Bangladesh Agricultural University in Mymensingh for phenotypic characterisation of 46 quinoa genotypes and genetic dissection of traits which are crucial for genetic improvement. The quantitative parameters studied are: days to maturity (DM), plant height (PH), panicle weight (PW), 1000-seed weight (TSW), above ground biomass (AGB), harvest index (HI) and yield per plant (YPP) showed substantial ($p \leq 0.01$) differences. Kaust-09755, Kaust-10860, Kaust-09386, Kaust-09385, Kaust-10810, Kaust-09379 and Kaust-10804 showed promising potential for yield improvements. Traits such as PH, PW, AGB and YPP exhibited high heritability and genetic advance. Yield per plant showed significant positive correlations with DM, PH, PW and AGB, with PW and AGB having the strongest direct impacts on yield. Genotypes were grouped into four distinct clusters, based upon D^2 analysis, with clusters III and IV being the most divergent. Principal component analysis (PCA) revealed that PC1 explained 55.10 % of the variability, with high positive loading for YPP, PW and AGB. Cluster and principal component analyses identified Kaust-05784, Kaust-09391, Kaust-10860 and SAU Quinoa-1 as highly divergent and suitable donor parents for future breeding programs.

Keywords: correlation coefficient; genetic advance; genetic diversity; heritability; path coefficient; PCA; quinoa; yield attributing traits

Introduction

Quinoa (*Chenopodium quinoa* L.) is a promising multifunctional pseudo-cereal that originated from the Andean region of South America (1). It is a facultative halophyte that belongs to the Amaranthaceae family (2). It was first domesticated by pre-Columbian cultures more than 7000 years ago (3), but was rejected as "Indian food" following the Spanish conquest (4). After centuries of neglect, quinoa has gained popularity in the last decade due to its exceptional nutritional value and ability to thrive in harsh and diverse environmental conditions (5). It is now cultivated in nearly 120 countries around the world (6).

Quinoa is considered as a superfood because of its high protein content and essential amino acid balance (7). Its grain has important nutritional qualities, such as high amounts of carbohydrate (64.2 g/100g), crude protein (11.7–16.7 g/100g), crude fat (3.49–6.8 g/100 g), crude fibre (3.95–11.5 g/100 g) and a balanced amount of minerals, essential and non-essential amino acids and bioactive substances like vitamins B2 and E, carotene, tocopherols. It also contains high levels of other molecules with antioxidant properties like flavonoids and other phenolic compounds (8, 9). It has numerous health benefits, including lowering blood pressure, helping to control diabetes, preventing heamorrhoids, promoting weight reduction, enhancing intestinal health and lowering the risk for cancer and heart disease (10). Quinoa's gluten-free nature makes it advantageous for those with wheat allergies and celiac disease (11). Though quinoa is primarily valued for its seeds, its leaves are as nutritious as the seeds, in some cases leaves are more nutritious than seeds and a previous study reported the potential use of quinoa as a leafy vegetable (9, 12). Quinoa leaves have a rich nutritional profile, surpassing other leafy greens like spinach, amaranth and moringa and also have potential pharmaceutical value as they contain high levels of bioactive compounds (13). Quinoa is a genetically diverse crop, which enables it to grow in a range of agro-ecological regions, including marginal lands with limited water availability, saline soils and areas with poor soil fertility (14, 15).

Climate change is putting enormous pressure on food systems, so it is essential to develop resilient crops that can survive in challenging environments to reduce yield losses. This is particularly crucial to maintain food security in the face of a world population that is expanding rapidly. Bangladesh, a climate-vulnerable nation,

faces significant agricultural issues like soil salinity and drought. In the southwestern coastal regions, 30 % of the arable land is affected by salinity (16), while drought causes substantial agricultural losses and seasonal food crises (17). Therefore, it is important to introduce crops like quinoa into Bangladesh to cultivate lands that are not cultivated at present, in the southern part of the country and to increase cropping intensity, which should boost GDP.

For successful integration of quinoa into a new geographical area, it is crucial to identify genetic differences between cultivars and to evaluate their region-specific agronomic potentials (18). This is because the phenotypic expression of different germplasm can vary significantly with changes in environmental conditions (19). In Bangladesh, a study investigated the agronomic performance of quinoa at different sowing dates (20). However, little has been done in Bangladesh to develop new genetically enhanced cultivars of quinoa. To develop a successful variety, breeders must assess a range of genotypes and comprehend the variability in the material to find superior genotypes (21). Genotypic and phenotypic variances, coupled with their coefficients of variation, provide essential insights into the interaction between a plant's genetic composition and environmental conditions that affect crop characteristics (22). This knowledge helps breeders prioritse traits for selection and this is fundamental to the success of crop improvement programs. In breeding programs, understanding heredity and genetic advances is imperative. Partitioning observed variability into heritable and non-heritable components is essential because the selection of good parents depends upon the extent to which the desirable traits are heritable (23). The primary constraint for quinoa cultivation in Bangladesh is the limited availability of a high-yielding quinoa variety.

Yield, being a complex trait, depends upon various yield-attributing traits. Therefore, correlation analysis is essential for understanding the relationships between yield and these attributing traits, as well as among the traits themselves (24). This helps identify which associations are essential to explain a crop's productivity potential. Simple correlations do not fully clarify the importance of each component trait in determining yield; path coefficient analysis is imperative to understand what partitions correlation coefficients into direct and indirect effects. This helps to provide a clearer understanding of the direct influence of each trait on yield and the indirect effects from mutual associations among traits (25). Moreover, multivariate statistical methods like principal component analysis (PCA) and D^2 analysis are used to streamline the data process and to reveal genetic diversity (26). PCA analysis helps to identify key traits that contribute the most to the overall variation in the dataset, while D^2 analysis groups similar data points based on their traits. This identifies distinct genetic clusters and enhances understanding of genetic diversity within a population, as well as helping breeders to choose genetically diverse parents for a successful hybridisation program.

The present study aimed to determine the degree of variability among exotic quinoa genotypes, estimate the nature and magnitude of genetic diversity in these genotypes based on yield attributing traits and also to identify potential genotype (s) for future plant breeding programs in Bangladesh. Consequently, the study aimed to answer the following question: how much genetic variation and heritable yield-related features do exotic quinoa genotypes exhibit when cultivated in Bangladeshi conditions? It was predicted that there would be significant genetic variability among the genotypes studied and that key agronomic variables would exhibit high heritability, providing opportunities for efficient selection and genetic advancement.

Materials and Methods

Plant materials, experimental site and season

A total of 46 quinoa genotypes were used in this study, including 2 varieties from Sher-e-Bangla Agricultural University in Bangladesh and Uzbekistan, 39 exotic lines from King Abdullah University of Science and Technology in Saudi Arabia and five advanced breeding lines from the University of Tasmania in Australia. The genotypes were chosen based upon their low saponin content, increased biomass and yield and resistance to drought and salinity and prior evidence from screening studies. The experiment was conducted in the field from November 2023 to March 2024 at the Agronomy Field Laboratory of the Department of Agronomy, Bangladesh Agricultural University, Mymensingh, Bangladesh. Sandy loam soil with a pH range of 6.5 to 6.7 was found at the experimental location, which was categorised as medium to high land within agro-ecological Zone-9 (Old Brahmaputra Flood Plain). Soil pH was measured using a glass electrode pH meter and soil texture was determined following the United States Department of Agriculture (USDA) protocol, by calculating the percentage of sand, silt and clay and plotting them on Marshall's triangular diagram. There are clear seasonal differences in the area, with the kharif (summer) season (April to October) characterised by high temperatures and plenty of rainfall and the rabi (winter) season (November to March) by lower temperatures and less precipitation. The average temperature, average humidity and total rainfall of the months during the experiment are shown in Supplementary Fig. 1.

Experimental design, layout and seed sowing

A RCBD with 3 replications had been used in the study. There were 46 experimental units in each block, each of which occupied a 14.4 m^2 (4 m × 3.6 m) plot and 12 rows in each plot, with a 30 cm row spacing and a 5 cm plant-to-plant spacing, following internationally accepted guidelines for quinoa phenotyping previously reported (27). On November 16, 2023, the seeds were sown in the moist soil using line sowing methods. Genotypes were allocated at random to plots inside each block using computer-generated randomisation.

Land preparation

The field was prepared through ploughing and cross-ploughing using a power tiller, followed by the removal of weeds and debris. To achieve a fine tilth and level surface, proper laddering was performed. The rates of fertiliser application were 172 kg of urea, 247 kg of TSP, 98 kg of MoP, 98 kg of gypsum, 5 kg of zinc and 5 kg of boron per hectare. Half of the urea, along with the full doses of all other fertilisers, was incorporated during the final land preparation, while the remaining half of the urea was top-dressed 25–30 days after sowing.

Intercultural operation

To promote the best possible plant growth, mild irrigation was given 30 days after the seeds were sown. Weeding and thinning were done 25 days following sowing to keep the plant-to-plant spacing consistent at 5 cm. Additional intercultural techniques were applied as required to ensure appropriate crop management and robust plant growth.

Harvest and postharvest operations

When almost 90 % of the grains had changed from yellow to deep brown, harvesting took place in February 2024. Five mature plants were chosen at random from each plot, sun-dried, threshed and then placed in net bags to continue drying. After cleaning, the seeds were sun-dried for 3 to 5 days to get a suitable moisture content. In the meantime, the above ground biomass was broken up and sun-dried for 3 to 5 days.

Data collection

A total of 7 quantitative traits (DM, PH, PW, TSW, AGB, HI and YPP) were recorded from 5 randomly selected plants of each genotype from each replication. These traits are widely reported as key determinants of yield and adaptation, particularly under South Asian agro-climatic conditions. Previous studies in Bangladesh and similar agro-climatic regions have identified these traits as key determinants of quinoa yield (28). To reduce border effects, data were collected from the central rows of each plot. This systematic random sampling ensured uniform representation of each genotype for trait evaluation.

Data analysis

A one-way analysis of variance (ANOVA) was used to identify differences across treatments and the Tukey's means comparison test was applied at a 5 % level of probability for the separation of significantly different mean values. Genetic parameters such as genotypic and phenotypic variances, genotypic and phenotypic coefficients of variation, heritability, genetic advance and percentage of the mean were estimated for biometrical analysis (29–31). Genotypic and phenotypic correlation coefficients and path coefficients were estimated according to the formula provided in previous studies (32, 33). Tocher's method was applied for non-hierarchical Euclidean cluster analysis, grouping genotypes into distinct clusters based on generalised inter and intra-cluster distances (D^2) (34). The study utilised multivariate PCA, introduced by Hotelling (35). To ensure the suitability of parametric analyses, the normality of trait distributions was assessed using histogram plots for all seven quantitative traits. The bell-shaped distributions observed indicated approximate normality of the data. These histograms are provided in Supplementary Fig. 2. R Statistical Package version 4.3.1 and Minitab version 18 were used for these biometrical analyses.

Results

Analysis of variance

Table 1 presents the results of the analysis of variance for 7 quantitative traits in quinoa. The mean square values for all studied traits exhibited highly significant variation ($p < 0.001$) among genotypes.

Mean performance analysis

The mean performance of 7 traits across 46 quinoa genotypes is presented in Table 2. Maturity varied significantly between genotypes, ranging from 107 days (Kaust-09609) to as early as 75 days (Kaust-10821). Interestingly, several genotypes, including Kaust-09436, SAU Quinoa-1 and GPBQ-2, reached maturity at approximately 78 days, indicating that they might be suitable for early cropping systems. The height of the plants also differed greatly; Kaust-05784 was the highest at 138 cm, while Kaust-10814 was the shortest at 38.83 cm, suggesting that the plant architectures were different. The genotype with the highest PW (39.22 g) was Kaust-10860. A cluster of high-performing genotypes was indicated by their similar performances (Kaust-09379, Kaust-09755, etc.). At the lower performance end, SAU Quinoa-1 and Kaust-10814 exhibited PWs below 8 g, highlighting potential yield limitations for these genotypes. Thousand seed weight showed less variation, with the highest TSW observed for Kaust-09391 (4.77 g), followed by a group of genotypes including Kaust-10800 and Kaust-10801. In contrast, TSW was lowest for GPBQ-3 and GPBQ-5 (2.57 g and 2.58 g, respectively), followed by GPBQ-1 (2.82 g), Kaust-09386 (3.11 g) and Kaust-10820 (3.12 g), where the difference was insignificant. The maximum amount of AGB was found for Kaust-10860 (53.05 g), while Kaust-09386 and Kaust-09379 both demonstrated excellent AGB. SAU Quinoa-1 and Kaust-10814, on the other hand, had the lowest biomass values (8.38 and 8.53 g, respectively), indicating little vegetative growth. It is interesting to note that despite their low biomass, these two genotypes, along with GPBQ-2, had the greatest HIs, surpassing 65 %, which suggests effective biomass partitioning into grain. On the contrary, the lowest value was observed in Kaust-05784 (44.65 %), followed by Kaust-09391 (47.92 %) and Kaust-10801 (49.41 %). A highly significant variation was observed for the trait YPP where the genotype Kaust-09755 showed the best performance (YPP 29.03 g), followed by Kaust-10860 (27.24 g), Kaust-09386 (26.09 g), Kaust-09385 (25.77 g), Kaust-10810 (25.23 g), Kaust-09379 (24.88 g) and Kaust-10804 (23.75 g), however, the differences among the genotypes are non-significant. The lowest YPP was recorded for Kaust-10814, SAU Quinoa-1 and Kaust-10843 (5.65 g, 5.85 g and 6.13 g, respectively).

Genetic parameter analysis

Genotypic and phenotypic variance, genotypic and phenotypic coefficient of variance, heritability, GA and GA % are shown in Table 3. In the present study, high genotypic and phenotypic variances were recorded in PH (306.29 and 325.72, respectively) and AGB (111.60 and 122.54, respectively) while the lowest were observed in TSW (0.18 and 0.20, respectively). The remaining traits exhibited moderate levels of genotypic and phenotypic variances. The coefficient analysis of variation represents that the phenotypic coefficient of variation (PCV) was higher than the genotypic coefficient of variation (GCV) for all the traits. The highest GCV and PCV were measured in PW (39.94 % and 41.60 %, respectively), AGB

Table 1. Analysis of variance (mean square) for yield and yield attributing traits on 46 quinoa genotypes

Sources of variation	DM	PH	PW	TSW	AGB	HI (%)	YPP
Replication	0.72	23.80	2.01	0.001	3.97	2.39	0.28
Genotype	101.5***	938.30***	189.91***	0.56***	345.73***	86.24***	103.52***
Error	1.36	19.42	5.22	0.02	10.95	10.91	3.18

*** indicates significant differences at 0.1% level of probability. Here, DM = Days to maturity (days), PH = Plant height (cm), PW = Panicle weight (g), TSW = Thousand seed weight (g), AGB = Above ground biomass (g), HI = Harvest index (%), YPP = Yield per plant (g).

Table 2. Mean performance of seven different traits of forty-six genotypes of quinoa

Genotypes name	DM	PH	PW	TSW	AGB	HI	YPP
Kaust-10811	90.66 f-h	97.26 b-e	25.35 cd	3.99 d-h	33.71 e-h	55.34 o-u	18.66 d-f
Kaust-10828	84.66 k	90.06 e-h	19.06 i-m	3.86 g-j	24.79 k-q	64.64 a-e	16.01 f-k
Kaust-10851	99.66 bc	82.60 h-l	23.37 d-h	3.53 l-p	35.72 ef	51.19 t-w	18.27 d-f
Kaust-09391	91.33 e-g	84.8 g-k	12.08 p-r	4.77 a	19.58 q-u	47.92 wx	9.37 p-r
Kaust-10820	85.33 k	78.96 i-m	16.26 l-o	3.12 t	20.93 o-t	63.57 a-h	13.28 k-n
Kaust-10793	90.00 g-j	78.60 i-m	24.28 d-f	3.55 l-p	32.17 f-i	61.75 c-l	19.88 d
Kaust-10799	91.00 e-g	97.06 b-e	19.80 h-l	3.38 o-s	27.88 i-m	53.10 q-w	14.78 h-l
Kaust-10860	90.66 f-h	102.40 bc	39.22 a	3.26 r-t	53.05 a	51.46 s-w	27.24 ab
Kaust-10800	85.33 k	45.93 rs	11.43 q-s	4.36 b	15.13 uv	51.91 r-w	7.86 q-s
Kaust-10834	93.66 d	93.16 d-g	12.35 pq	3.94 e-h	17.17 tu	61.65 c-l	10.54 o-q
Kaust-10824	85.33 k	71.20 m-o	16.53 l-o	3.47 m-r	21.7 n-t	63.88 a-g	13.82 j-m
Kaust-09755	98.00 c	85.10 g-j	35.32 b	3.34 p-s	46.7 bc	62.29 c-k	29.03 a
Kaust-09805	90.66 f-h	89.06 e-h	21.41 f-j	3.30 q-t	27.75 i-m	59.21 f-o	16.42 f-j
Kaust-10835	88.33 j	81.86 h-l	15.65 m-p	3.59 k-o	20.87 o-t	60.98 c-m	12.71 l-o
Kaust-10818	90.66 f-h	86.60 f-i	19.69 h-l	3.48 l-q	26.18 j-o	62.57 c-j	16.37 f-j
Kaust-09436	78.66 l	74.73 l-n	20.50 g-k	3.60 k-n	26.48 j-n	60.31 d-o	15.96 f-k
Kaust-10843	91.00 e-g	58.80 pq	8.31 st	3.36 p-s	10.54 vw	58.28 h-q	6.13 s
Kaust-09417	92.33 d-f	68.86 no	15.73 m-p	3.36 p-s	20.55 p-t	61.73 c-l	12.68 l-o
Kaust-10864	92.66 de	93.60 c-g	21.73 d-i	3.50 l-q	30.75 f-j	56.93 k-r	17.51 d-h
Kaust-10792	85.66 k	65.40 op	12.44 pq	3.85 g-j	16.86 tu	60.75 c-n	10.26 o-q
Kaust-05784	99.66 bc	138.00 a	17.73 j-n	3.90 f-i	32.07 f-i	44.65 x	14.31 j-m
Kaust-10801	88.66 ij	83.00 h-l	14.19 n-q	4.32 bc	21.00 o-t	49.41 v-x	10.38 o-q
Kaust-10839	90.33 g-i	87.00 f-i	22.91 d-h	3.94 e-h	30.54 f-j	58.08 i-q	17.76 d-g
Kaust-09387	90.66 f-h	86.73 f-i	25.14 de	3.46 m-r	34.22 e-g	57.44 j-q	19.64 de
Kaust-09386	92.66 de	100.46 b-d	34.76 b	3.11 t	48.88 ab	53.69 p-v	26.09 bc
Kaust-10830	90.66 f-h	102.90 b	21.51 e-i	3.17 st	28.78 h-l	59.30 e-o	17.08 e-h
Kaust-10814	85.66 k	38.83 s	7.02 t	3.78 h-k	8.38 w	68.66 a	5.65 s
Kaust-09244	90.66 f-h	50.33 qr	19.86 h-l	4.13 c-e	26.96 i-n	51.56 s-w	13.90 j-m
Kaust-09464	92.66 de	90.66 e-h	22.90 d-h	3.66 j-m	30.15 g-k	56.55 l-t	17.06 e-i
Kaust-10816	86.00 k	68.73 no	16.51l m-o	4.18 b-d	22.75 m-s	63.12 b-i	14.34 i-m
Kaust-10804	91.00 e-g	95.33 b-f	28.96 c	3.62 k-n	38.1 de	62.42 c-j	23.75 c
Kaust-09385	89.00 h-j	77.10 j-n	34.17 b	3.54 l-p	43.68 bc	59.66 e-o	25.77 bc
kaust-09390	90.33 g-i	94.73 b-f	14.07 n-q	3.50 l-q	19.72 q-u	55.44 n-u	10.93 n-p
Kaust-09609	107.00 a	59.00 pq	18.74 i-m	3.98 d-h	23.22 m-r	65.48 a-d	15.14 g-l
Kaust-10810	90.66 f-h	92.66 d-g	33.13 b	3.70 i-l	42.60 cd	59.33 e-o	25.23 bc
Kaust-10821	75.33 m	70.76 m-o	13.42 o-q	3.87 g-j	17.64 s-u	61.44 c-l	10.72 n-p
Kaust-10794	90.66 f-h	88.58 e-h	14.82 n-q	3.63 k-n	19.65 q-u	59.37 e-o	11.67 m-p
Kaust-09384	91.66 e-g	75.66 l-n	18.65 i-m	3.78 h-k	25.57 j-p	55.72 m-u	14.25 j-m
Kaust-09379	100.66 b	99.53 b-d	35.44 b	3.94 e-h	48.74 ab	51.08 u-w	24.88 bc
SAU-1	78.66 l	58.40 pq	6.73 t	4.10 d-f	8.53 w	68.32 ab	5.85 s
Regalona	92.33 d-f	94.06 c-f	17.56 k-n	3.43 n-r	24.23 l-q	58.60 g-p	14.20 j-m
GPBQ-1	85.66 k	76.16 k-n	13.02 o-q	2.82 u	17.99 r-u	57.97 i-q	10.32 o-q
GPBQ-2	78.66 l	53.53 qr	8.52 r-t	4.06 d-g	10.40 vw	65.67 a-c	6.83 rs
GPBQ-3	85.66 k	78.86 i-m	11.79 q-s	2.57 v	16.39 tu	56.59 l-s	9.23 p-r
GPBQ-4	85.00 k	75.83 l-n	17.57 k-n	3.67 j-m	23.69 l-q	64.32 a-f	15.20 g-l
GPBQ-5	90.66 f-h	68.43 no	23.84 d-g	2.58 v	29.91 g-k	62.47 c-j	18.68 d-f
Mean	89.70	81.11	19.64	3.63	26.57	58.60	15.34
Range	75.33-107.00	38.83-138.00	6.73-39.22	2.57-4.77	8.38-53.05	44.65-68.66	5.65-29.03
CV %	1.30	6.69	11.64	3.71	12.45	5.63	10.97
LSD	1.89	8.81	3.71	0.21	5.36	5.35	2.73
SE	0.67	3.13	1.32	0.07	1.91	1.90	0.97

DM = Days to Maturity (days), PH = Plant height (cm), PW = Panicle weight (g), TSW = Thousand seed weight (g), AGB = Above ground biomass (g), HI = Harvest index (%), YPP = Yield per plant (g). CV = Coefficient of variation (%), LSD = Least significant difference, SE = Standard error

Different letters in each column show statistically significant differences among the evaluated variables.

Table 3. Estimation of genetic parameters for morphological traits related to yield in 46 quinoa genotypes

Characters	Genotypic variance (σ^2_g)	Phenotypic variance (σ^2_P)	GCV (%)	PCV (%)	Heritability in broad sense (h^2b) (%)	GA	GA (%)
DM	33.40	34.77	6.44	6.57	96	11.67	13.01
PH	306.29	325.72	21.57	22.25	94	34.96	43.10
PW	61.56	66.79	39.94	41.60	92	15.52	78.99
TSW	0.18	0.20	11.71	12.28	91	0.84	23.00
AGB	111.60	122.54	39.75	41.65	91	20.77	78.14
HI (%)	25.11	36.02	8.55	10.24	70	8.62	14.70
YPP	33.45	36.63	37.74	39.50	91	11.38	74.29

DM = Days to Maturity (days), PH = Plant height (cm), PW = Panicle weight (g), TSW = Thousand seed weight (g), AGB = Above ground biomass (g), HI = Harvest index (%), YPP = Yield per plant (g), GCV = Genetic co-efficient of variance, PCV = Phenotypic co-efficient of variance, GA = Genetic advance, GA% = Genetic advance as percentage of mean.

(39.75 % and 41.65 %, respectively), YPP (37.74 % and 39.50 %, respectively) and PH (21.57 % and 22.25 %, respectively) while the lowest GCV and PCV values were obtained for DM (6.44 % and 6.57 %, respectively) and HI (8.55 % and 10.24 %, respectively). Notably, PW, AGB, YPP and HI showed a higher difference between GCV and PCV, whereas DM and TSW exhibited a lower difference. The heritability analysis in the broad sense revealed that almost all the traits were highly heritable (70–96 %). Genetic advance as a percentage of the mean was high for the traits PW (78.99 %), AGB (78.14 %), YPP (74.29 %), PH (43.10 %) and TSW (23.00 %) and moderate for HI (14.70 %) and DM (13.01 %). Significantly, PW, AGB and YPP exhibited both high heritability and a high GA %. The confidence intervals of genetic parameters for seven quantitative traits of quinoa are shown in the Supplementary Table 1.

Phenotypic and genotypic correlation coefficients of yield and yield attributing traits

The results of phenotypic and genotypic correlation coefficients of yield and yield attributing traits of quinoa are presented in Table 4. The correlation analysis showed that genotypic correlation coefficients were higher than phenotypic correlation coefficients for almost all the traits. In the current study, YPP demonstrated a significant positive correlation at both the genotypic and phenotypic levels with DM (r_p = 0.41**; r_g = 0.45**), PH (r_p = 0.48**; r_g = 0.49**), PW (r_p = 0.98**; r_g = 0.99**) and AGB (r_p = 0.96**; r_g= 0.97**). In contrast, it exhibited a significant negative correlation with TSW (r_p = -0.25**) only at the phenotypic level. Both phenotypic and genotypic levels of DM showed a significant correlation with PH (r_p = 0.39**; r_g = 0.41**) and PW (r_p = 0.42**; r_g = 0.45**). While PH exhibited a significant negative association with TSW (r_p = -0.17*) only at the phenotypic level, it showed a significant positive connection with PW (r_p = 0.48**; r_g = 0.49**) and AGB (r_p = 0.56**; r_g= 0.57**) at both the genotypic and phenotypic levels. PW also showed significant positive correlation with AGB (r_p= 0.98** and r_g= 0.98**) at both phenotypic and genotypic levels and significant negative correlation with TSW (r_p= -0.22**), only at the phenotypic level. HI showed a negative correlation with all other traits. It was recorded that HI was significantly negatively correlated with DM (r_p= -0.33** and r_g= -0.42**), PH (r_p= -0.46** and r_g= -0.53**) and AGB (r_p= -0.33** and r_g= -0.36*) at both phenotypic and genotypic levels and with PW (r_p= -0.21**) at only phenotypic levels. Other trait associations were not statistically significant.

Phenotypic and genotypic path coefficient analysis

The results of phenotypic and genotypic path coefficient analysis indicating the relationship between yield and yield attributing traits are presented in Table 5. At both phenotypic and genotypic levels, PW and AGB exhibited the highest positive direct effects on yield per plant. The direct effects of PW were r_{yp} = 0.45382 and r_{yg}= 0.39539, while AGB showed even higher direct contributions with values of r_{yp} = 0.55821 and r_{yg}= 0.62235. These traits also contributed substantial positive indirect effects through most of the associated traits, particularly through each other. The phenotypic and genotypic path analysis showed higher positive indirect effects on YPP via PW from AGB (r_{yp} = 0.44633 and r_{yg}= 0.3907), PH (r_{yp} = 0.21856 and r_{yg}= 0.19469) and DM (r_{yp} = 0.19133 and r_{yg}= 0.17993). Through AGB, traits such as PW (r_{yp} = 0.549 and r_{yg}= 0.61497), PH (r_{yp} = 0.31773 and r_{yg}= 0.36056) and DM (r_{yp} = 0.26236 and r_{yg}= 0.31753) exhibited high positive indirect effects, while TSW (r_{yp} = -0.11069 and r_{yg}= -0.13539) and HI (r_{yp} = -0.18583 and r_{yg}= -0.22918) showed high negative indirect effects.

DM (r_{yp} = 0.0183 and r_{yg}= 0.02181) and PH (r_{yp} = 0.01295 and r_{yg}= 0.01247) showed comparatively smaller but positive direct effects on YPP at both phenotypic and genotypic levels. In contrast,

Table 4. Correlation coefficients of yield and yield contributing traits

Characters		PH	PW	TSW	AGB	HI (%)	YPP
DM	r_p	0.39**	0.42**	-0.03	0.47**	-0.33**	0.41**
	r_g	0.41**	0.45**	-0.04	0.51**	-0.42**	0.45**
PH	r_p		0.48**	-0.17*	0.56**	-0.46**	0.48**
	r_g		0.49**	-0.16	0.57**	-0.53**	0.49**
PW	r_p			-0.22**	0.98**	-0.21*	0.98**
	r_g			-0.25	0.98**	-0.25	0.99**
TSW	r_p				-0.19*	-0.15	-0.25**
	r_g				-0.21	-0.21	-0.27
AGB	r_p					-0.33**	0.96**
	r_g					-0.36*	0.97**
HI (%)	r_p						-0.11
	r_g						-0.17

* and ** indicate significance at 5 % and 1 % level of probability respectively

Here, DM = Days to maturity (days), PH = Plant height (cm), PW = Panicle weight (g), TSW = Thousand seed weight (g), AGB = Above ground biomass (g), HI = Harvest index (%), YPP = Yield per plant (g)

r_p=phenotypic correlation coefficient and r_g=genotypic correlation coefficient

Table 5. Partitioning of phenotypic and genotypic correlations into direct and indirect effects of seven important traits related to yield by path analysis

Characters		DM	PH	PW	TSW	AGB	HI (%)	YPP Correlation coefficient
DM	r_{yp}	**0.0183**	0.01295	0.19133	0.00002	0.26236	-0.06506	0.41**
	r_{yg}	**0.02181**	0.01247	0.17993	-0.00008	0.31753	-0.07431	0.45**
PH	r_{yp}	0.00716	**0.03312**	0.21856	0.00012	0.31773	-0.08939	0.48**
	r_{yg}	0.00904	**0.03008**	0.19469	-0.00032	0.36056	-0.09415	0.49**
PW	r_{yp}	0.00771	0.01595	**0.45382**	0.00016	0.549	-0.04094	0.98**
	r_{yg}	0.00993	0.01481	**0.39539**	-0.00048	0.61497	-0.04435	0.99**
TSW	r_{yp}	-0.00056	-0.00577	-0.10411	**-0.0007**	-0.11069	-0.02908	-0.25**
	r_{yg}	-0.00089	-0.00508	-0.09965	**0.00192**	-0.13539	-0.03708	-0.27
AGB	r_{yp}	0.0086	0.01885	0.44633	0.00014	**0.55821**	-0.06423	0.96**
	r_{yg}	0.01113	0.01743	0.3907	-0.00042	**0.62235**	-0.06493	0.97**
HI (%)	r_{yp}	-0.00617	-0.01534	-0.0963	0.00011	-0.18583	**0.19294**	-0.11
	r_{yg}	-0.00919	-0.01606	-0.09944	-0.0004	-0.22918	**0.17632**	-0.17

Diagonally bold figures indicate the direct effect; Residual effect for phenotypic path-coefficient = 0.0097 & Residual effect for genotypic path-coefficient = 0.0078. ** indicates significance at 1 % level of probability. DM = Days to maturity (days), PH = Plant height (cm), PW = Panicle weight (g), TSW =Thousand seed weight (g), AGB = Above ground biomass (g), HI = Harvest index (%), YPP = Yield per plant (g).

r_{yp}= Phenotypic path-coefficient and r_{yg}= Genotypic path-coefficient

TSW exhibited a very small negative direct effect on yield per plant at the phenotypic level (r_{yp} = -0.0007), while its genotypic direct effect was positive but negligible (r_{yg}= 0.00192). The indirect effects of TSW through other traits were largely negative, resulting in an overall negative correlation with yield per plant. HI showed a positive direct effect at both phenotypic (r_{yp} = 0.19294) and genotypic (r_{yg}= 0.17632) levels; however, its indirect effects through most traits were negative, leading to a weak and negative overall association with yield per plant. The phenotypic and genotypic residual effects were 0.0097 and 0.0078, respectively.

D^2 analysis

The experimental population was divided into 4 clusters based on their distribution pattern using D^2 analysis. The hierarchical dendrogram of 46 genotypes is displayed in Fig. 1. The genotypes of each cluster and their sources are shown in Table 6. The largest of the 4 groups, cluster II, contained 20 genotypes. Cluster I, on the other hand, contained 15 genotypes, cluster IV, seven and cluster III, the smallest, contained just four. The degree of divergence inside and between the groupings is indicated by the average intra- and inter-cluster distances in Fig. 2. Cluster III and cluster IV had the

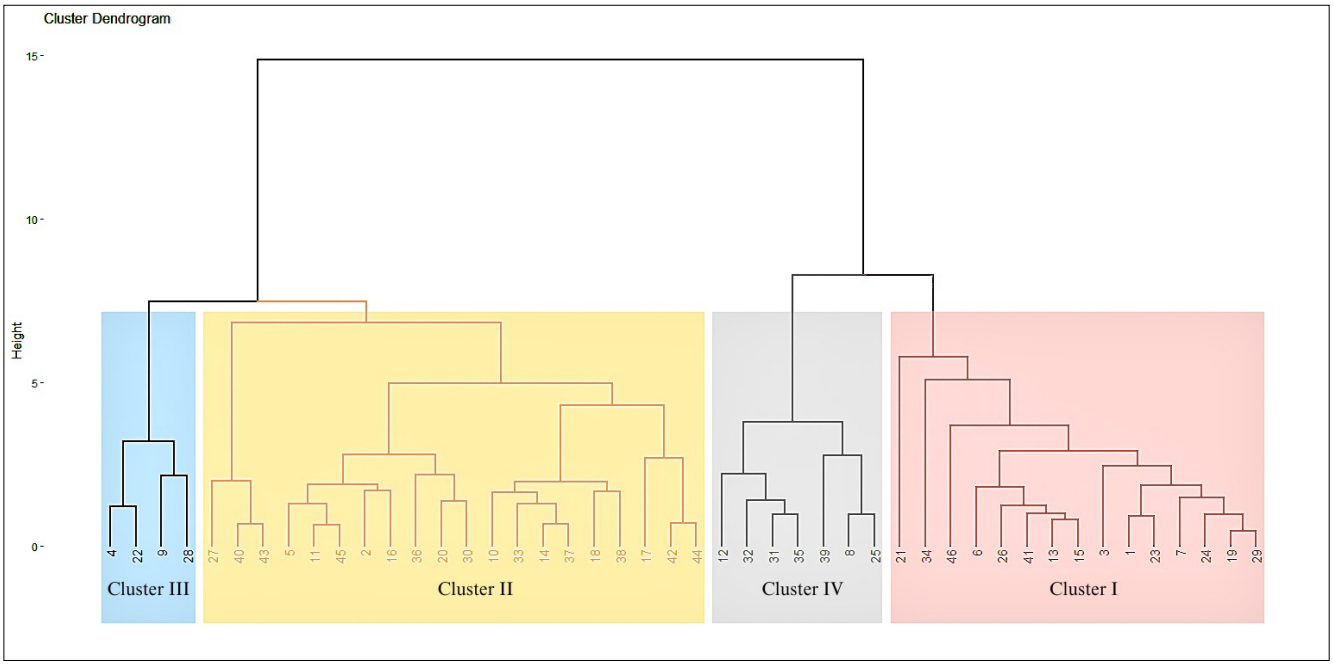

Fig. 1. Hierarchical Wards method dendrogram of 46 quinoa genotypes displaying various cluster groups.

1=Kaust-10811, 2=Kaust-10828, 3=Kaust-10851, 4=Kaust-09391, 5=Kaust-10820, 6=Kaust-10793, 7=Kaust-10799, 8=Kaust-10860, 9=Kaust-10800,10=Kaust-10834, 11=Kaust-10824, 12=Kaust-09755, 13=Kaust-09805, 14=Kaust-10835, 15=Kaust-10818, 16=Kaust-09436, 17=Kaust-10843, 18=Kaust-09417, 19=Kaust-10864, 20=Kaust-10792, 21=Kaust-05784, 22=Kaust-10801, 23=Kaust-10839, 24=Kaust-09387, 25=Kaust-09386, 26=Kaust-10830, 27=Kaust-10814, 28=Kaust-09244, 29=Kaust-09464, 30=Kaust-10816, 31=Kaust-10804, 32=Kaust-09385, 33=kaust-09390, 34=Kaust-09609, 35=Kaust-10810, 36=Kaust-10821, 37=Kaust-10794, 38=Kaust-09384, 39=Kaust-09379, 40=SAU Quinoa-1, 41=Ragalona, 42=GPBQ-1, 43=GPBQ-2, 44=GPBQ-3, 45=GPBQ-4 and 46=GPBQ-5

Table 6. Clustering pattern of 46 quinoa genotypes by Euclidean distance method

Cluster no.	Total no. of genotypes	Genotypes	Sources
I	15	Kaust-05784	KAUST, Saudi Arabia
		Kaust-09609	KAUST, Saudi Arabia
		GPBQ-5	University of Tasmania, Australia
		Kaust-10793	KAUST, Saudi Arabia
		Kaust-10830	KAUST, Saudi Arabia
		Ragalona	Uzbekistan
		Kaust-09805	KAUST, Saudi Arabia
		Kaust-10818	KAUST, Saudi Arabia
		Kaust-10851	KAUST, Saudi Arabia
		Kaust-10811	KAUST, Saudi Arabia
		Kaust-10799	KAUST, Saudi Arabia
		Kaust-10839	KAUST, Saudi Arabia
		Kaust-09387	KAUST, Saudi Arabia
		Kaust-10864	KAUST, Saudi Arabia
		Kaust-09464	KAUST, Saudi Arabia
		Kaust-10814	KAUST, Saudi Arabia
II	20	SAU Quinoa-1	Sher-e-Bangla Agricultural University
		GPBQ-2	University of Tasmania, Australia
		GPBQ-4	University of Tasmania, Australia
		Kaust-10820	KAUST, Saudi Arabia
		Kaust-10824	KAUST, Saudi Arabia
		Kaust-10828	KAUST, Saudi Arabia
		Kaust-10818	KAUST, Saudi Arabia
		Kaust-10792	KAUST, Saudi Arabia
		Kaust-10821	KAUST, Saudi Arabia
		Kaust-10816	KAUST, Saudi Arabia
		Kaust-10834	KAUST, Saudi Arabia
		Kaust-10835	KAUST, Saudi Arabia
		kaust-09390	KAUST, Saudi Arabia
		Kaust-10794	KAUST, Saudi Arabia
		Kaust-09384	KAUST, Saudi Arabia
		Kaust-09417	KAUST, Saudi Arabia
		Kaust-10843	KAUST, Saudi Arabia
		GPBQ-1	University of Tasmania, Australia
		GPBQ-3	University of Tasmania, Australia
III	4	Kaust-09391	KAUST, Saudi Arabia
		Kaust-10800	KAUST, Saudi Arabia
		Kaust-10801	KAUST, Saudi Arabia
		Kaust-09244	KAUST, Saudi Arabia
IV	7	Kaust-09755	KAUST, Saudi Arabia
		Kaust-09385	KAUST, Saudi Arabia
		Kaust-10804	KAUST, Saudi Arabia
		Kaust-10810	KAUST, Saudi Arabia
		Kaust-09379	KAUST, Saudi Arabia
		Kaust-10860	KAUST, Saudi Arabia
		Kaust-09386	KAUST, Saudi Arabia

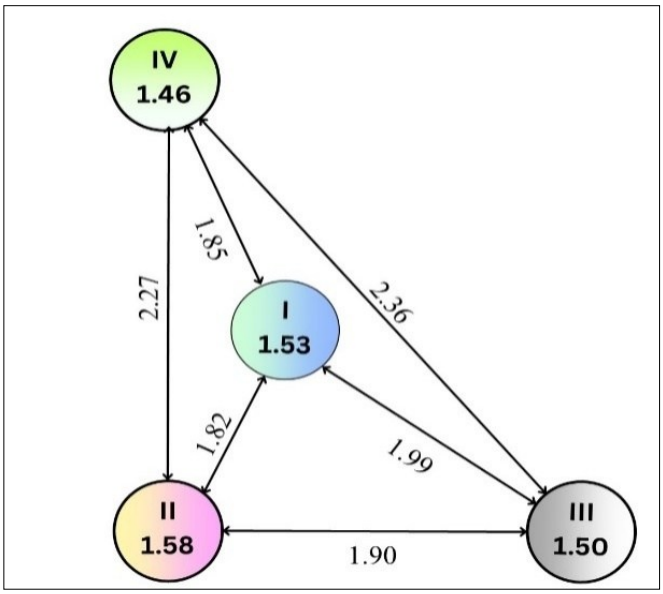

Fig. 2. Cluster diagram showing average intra- and inter-cluster distance ($D=\sqrt{D^2}$ values) of the quinoa genotypes.

The values among the lines indicate inter-cluster distance and the values in the circle indicate intra-cluster distance

greatest inter-cluster distances (2.36), followed by cluster II and cluster IV (2.27). Cluster II had the greatest intra-cluster distance (1.58), followed by cluster I (1.53) and cluster III (1.50).

The average performance of each cluster for each trait is presented in Table 7. The genotypes of cluster IV showed the highest performance for PH (93.23 cm), PW (34.43 g), AGB (45.97 g), HI (57.14 %) and YPP (26 g). Cluster I also showed high values for PH (90.11 cm) and HI (57.52 %). Cluster II and cluster III had the greatest TSWs, measuring 4.40 and 3.61 g, respectively. Clusters IV and I had significantly higher YPP values, at 26 and 17.06 g , respectively.

Principal component analysis

A principal component analysis considering 7 quantitative traits across 46 quinoa genotypes is presented in Table 8. 94.24 % of the overall variation was attributed to the first 4 components, according to the results. Notably, 73.97 % of the entire variation was explained by the first two PC, whose cumulative eigenvalues were greater than 1. In particular, 55.10 % of the variation was explained by PC1, with PC2 (18.87 %), PC3 (11.63 %) and PC4 (8.63 %) following closely behind. In the first PC, AGB, PW and YPP had the highest positive loading (0.50, 0.48 and 0.47, respectively), while the negatively loaded traits were TSW (-0.13) and HI (%) (-0.20). The second PC was

Table 7. Cluster mean of 7 quantitative traits of 46 quinoa genotypes

Characters	Clusters			
	I	II	III	IV
DM	93.29	85.92	89.00	93.24
PH	90.11	73.16	66.02	93.23
PW	21.73	13.95	14.39	34.43
TSW	3.53	3.61	4.40	3.50
AGB	29.82	18.54	20.67	45.97
HI (%)	57.52	61.63	50.20	57.14
YPP	17.06	11.32	10.38	26.00

DM = Days to Maturity (days), PH = Plant Height (cm), PW = Panicle weight (g), TSW = Thousand seed Weight (g), AGB = Above ground biomass (g), HI = Harvest index (%), YPP = Yield per plant (g).

Table 8. Principal components (PCs) for yield and yield-related traits in 46 quinoa genotypes from PCA with Eigen vectors (loadings) of the first four PCs

Variables	PC1	PC2	PC3	PC4
DM	0.30	0.29	0.02	0.90
PH	0.35	0.25	0.43	-0.24
PW	0.48	-0.18	-0.24	-0.11
TSW	-0.13	0.54	-0.76	-0.11
AGB	0.50	-0.07	-0.17	-0.13
HI (%)	-0.20	-0.67	-0.27	0.27
YPP	0.47	-0.24	-0.24	-0.06
Eigenvalue	3.85	1.321	0.81	0.60
%Variation explained	55.10%	18.87%	11.63%	8.63%
Cumulative variance (%)	55.10%	73.97%	85.60%	94.24%

DM = Days to Maturity (days), PH = Plant height (cm), PW = Panicle weight (g), TSW = Thousand seed weight (g), AGB = Above ground biomass (g), HI = Harvest index (%), YPP = Yield per plant (g).

positively influenced by the trait TSW, DM and PF (0.54, 0.29 and 0.25, respectively) and negatively influenced by PW, AGB, HI and YPP (-0.18, -0.07, -0.67 and -0.24 ,respectively).

The PCA biplot showing quinoa genotype clusters in PC1 and PC2 is presented in Fig. 3. It revealed that 41 (Ragalona) and 34 (Kaust-09609) were the most stable genotype as they were the closest to the origin, while 21 (Kaust-05784), 40 (SAU Quinoa-1), 8 (Kaust-10860) and 4 (Kaust-09391) were the least stable genotypes. The research also revealed that the features YPP, PW and AGB had higher values in genotypes 6, 8, 12, 13, 15, 24, 25, 26, 31, 32, 35 and 46. However, in genotypes 1, 3, 7, 19, 21, 23, 29, 39 and 41, PH and DM

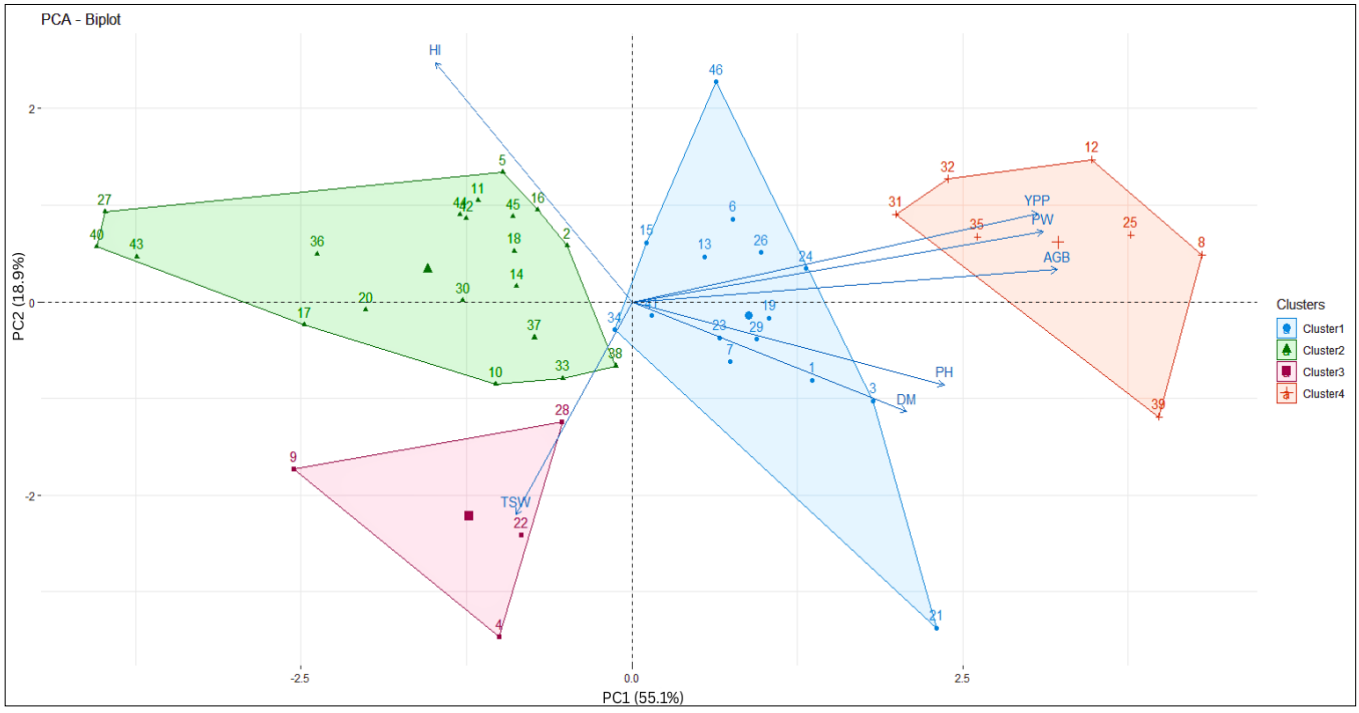

Fig. 3. PCA biplot showing quinoa genotype clusters in PC1 and PC2.

1=Kaust-10811, 2=Kaust-10828, 3=Kaust-10851, 4=Kaust-09391, 5=Kaust-10820, 6=Kaust-10793, 7=Kaust-10799, 8=Kaust-10860, 9=Kaust-10800,10=Kaust-10834, 11=Kaust-10824, 12=Kaust-09755, 13=Kaust-09805, 14=Kaust-10835, 15=Kaust-10818, 16=Kaust-09436, 17=Kaust-10843, 18=Kaust-09417, 19=Kaust-10864, 20=Kaust-10792, 21=Kaust-05784, 22=Kaust-10801, 23=Kaust-10839, 24=Kaust-09387, 25=Kaust-09386, 26=Kaust-10830, 27=Kaust-10814, 28=Kaust-09244, 29=Kaust-09464, 30=Kaust-10816, 31=Kaust-10804, 32=Kaust-09385, 33=kaust-09390, 34=Kaust-09609, 35=Kaust-10810, 36=Kaust-10821, 37=Kaust-10794, 38=Kaust-09384, 39=Kaust-09379, 40=SAU Quinoa-1, 41=Ragalona, 42=GPBQ-1, 43=GPBQ-2, 44=GPBQ-3, 45=GPBQ-4 and 46=GPBQ-5

Cluster 1–4 represent genotype groups based on their distribution patterns

were more common. Genotypes 4, 9, 10, 17, 20, 22, 28, 33, 34, 37 and 38 showed higher TSW, whereas genotypes 2, 5, 11, 14, 16, 18, 27, 30, 36, 40, 42, 43, 44 and 45 showed higher HI.

Discussion

Analysis of variance

The growing demand for quinoa highlights the need to develop high-yielding varieties and this requires the characterisation of diverse genotypes. Significant variability (p < 0.001) among genotypes for 7 traits (DM, PH, PW, TSW, AGB, HI and YPP), as shown in Table 1, indicates the potential for genetic improvement through selective breeding. Similar findings of trait variability were previously reported (36). Targeting these traits can help breeders develop high-yielding quinoa varieties to meet increasing demand.

Mean performance analysis

From the mean performance of 46 quinoa genotypes for 7 traits (Table 2), it was shown that plants matured on average 89 days after sowing, with DM ranging from 75 to 107 days. While a previous study reported a longer mean of 116 days (range: 95–150 days) (37). The genotypes used in the present trial were mostly short-duration cultivars, such as Kaust-10821, which developed in just 75 days and Kaust-09436, SAU Quinoa-1 and GPBQ-2, each of which took 78 days. These early-maturing genotypes hold great promise for producing quinoa varieties that are appropriate for areas that experience drought and have shorter growing seasons or require several cropping cycles in a single year. With an average height (PH) of 81.11 cm and a range of 38.83 to 138.00 cm, the genotypes used in the present study showed considerable variation in PH. This variation may be useful for breeding objectives, for example, the production of tall biomass-rich lines or shorter lodging resistance lines. This finding is similar to the observations of previous studies (37, 38). Genotypes also varied significantly in AGB and PW. While AGB ranged from 8.38 to 53.05 g, with an average of 26.57 g, PW ranged from 6.73 to 39.22 g, with an average of 19.64 g. A study from 2007 reported that AGB ranged from 1.11 g to 52.89 g (39). According to another study, the TSW of genotypes ranged from 2.57 g to 4.77 g, with a mean of 3.63 g (37). The HI of genotypes ranged from 44.65 to 68.66 %, with an average of 58.60 %. This is greater than the mean HI of 40 % obtained in a previous study (37). Quinoa generally has low average HI values, which is caused by a higher assimilate allocation to vegetative biomass rather than to seeds, particularly in genotypes that mature late (40). Prolonged vegetative growth increases respiration losses and reduces resources for grain filling. A significant variation in YPP was found in the genotypes used in the present study, which ranged from 5.65 to 29.03 g with an average of 15.34 g. This was similar to previous works, which reported that the YPP mean was 15 g (41). In contrast, another study reported a much lower mean YPP of 4.06 g. These results indicate the existence of genotypes with high yield potential, which could contribute to the development of high-yielding quinoa varieties.

Genetic parameter analysis

The effectiveness of a crop breeding program is primarily dependent upon genetic variation and the inheritance patterns of the traits under consideration. Phenotypic variance (σ^2p) generally exceeds genotypic variance (σ^2g) as it includes both genotypic and environmental variance. In this study, PCV values were slightly higher than GCV values for all traits (Table 3), indicating a minor environmental influence and a predominant genetic influence. These findings are significant for breeders as they offer guidance when selecting suitable breeding strategies, thereby aiding in the enhancement of target traits in crops more effectively. GCV and PCV values can be categorised as low (< 10 %), moderate (10–20 %) and high (> 20 %) (42). In the present study, PW, AGB, YPP and PH showed higher GCV and PCV values (Table 3), indicating a broad genetic base and considerable potential for genetic improvement of these traits. In contrast, DM and HI showed low PCV and GCV values (Table 3), which indicates that selection is not effective for these traits because of the limited variation. A previous study also found high PCV and GCV values for PH and YPP and low values for DM, aligning with the results of the present study (39).

The h^2b and genetic advance for seven quantitative traits are presented in Table 3 and heritability can be categorised as low (0–30 %), medium (31–60 %) and high (> 60 %) (31). A high heritability indicates that a large proportion of the observed variation in a trait is due to genetic differences among individuals, with a little influence of environment, which makes the selection of that trait effective for genetic improvement. Based upon these categories, all the traits investigated in the present study exhibit high heritability (Table 3), suggesting that these traits can be selected for very effectively across various environments due to minimal environmental influence.

High heritability alone cannot lead to large genetic gains; however, when combined with high genetic advance (GA %), it indicates a strong genetic influence and the potential for improvement through selection. Genetic advance as a percent of mean (GA %) can be categorised as low (< 10 %), moderate (10–20 %) or high (> 20 %) (31). AGB, YPP, PW and PH all showed high heritability and a high GA % in this study, indicating that additive gene action is primarily responsible for controlling these traits. Additive genes are inherited from parents in a predictable way and regularly contribute to the phenotype, so these traits can be effectively enhanced through simple selection methods. Similar results were determined in a previous study (39). In contrast, high heritability coupled with moderate GA % was observed for DM and HI, indicating non-additive genetic effects. Complex gene interactions influence phenotypes due to non-additive gene effects, including dominance and epistasis, which makes it more difficult to predict offspring performance based upon parental features. Furthermore, some characteristics change depending on the environment due to genotype × environment interactions. When combined, these elements lessen the validity of choosing plants only based on visible characteristics. To find and preserve the best gene combinations for continuous improvement, breeding techniques such as hybridisation, followed by progeny testing are required.

Phenotypic and genotypic correlation coefficients between yield and yield-attributing traits

Yield is a complex quantitative trait that is dependent upon the cumulative effect of many genes and is influenced by various interrelated morphological traits. Correlation analysis helps to identify the best trait combination for high yield by quantifying the degree of association of different traits with yield and with each other. While phenotypic correlation shows the apparent association between qualities, impacted by both genetic and environmental factors, genotypic correlation shows the genetic relationships between traits. Stronger genotypic correlations in this study suggest

a higher level of genetic influence, reflecting the possibility that desirable traits could be enhanced by indirect selection.

Correlation of seed yield with other yield-related traits

In the present study, YPP showed a strong positive correlation (p<0.01) with DM, PH, PW and AGB (Table 4), indicating a synergistic relationship contributing to yield improvement. Similar positive correlations between YPP and PH, AGB and DM were reported in a previous research (43). Conversely, a previous study found negative correlations of YPP with PH and DM, likely due to variations in genotypes and environmental conditions (44). Temperature and photoperiod both significantly affect leaf elongation and total plant growth, as demonstrated in a previous research (45). To absorb more light, plant leaves typically enlarge when exposed to longer days and greater radiation levels. Higher yields and improved growth are the result of greater photosynthetic activity brought by the increased light interception. Consequently, plants that mature later, when exposed to longer photoperiods and more radiation, generally yield more. Taller plants also frequently produce more seeds because they have more branches and nodes that contain panicles. Larger or more numerous seeds are indicated by heavier panicles and robust vegetative development and higher assimilate production is indicated by increased above-ground biomass. Greater above-ground biomass indicates a greater source of assimilates available for grain filling. These factors both improve yield by better allocating resources to reproductive structures.

Additionally, there was a significant negative correlation (p<0.01) between YPP and TSW at the phenotypic level (Table 4), implying that TSW tends to decrease as YPP increases. This suggests a trade-off between seed size and seed number, where increased yield is achieved primarily through the production of more seeds rather than larger seeds. This is in contrast to the findings from other studies that highlight the strong influence of genotype and environment on yield components (43, 44). Overall, these findings suggest that, for breeding higher-yielding quinoa, genotypes with greater AGB, taller plants, higher PW and later maturity should all be selected for.

Correlation among other yield-related traits

From the data represented in Table 4, it is clear that DM had a significant positive correlation (p<0.01) with PH, PW and AGB. These findings are supported by previous studies (39, 43). Conversely, HI showed a significant negative correlation (p<0.01) with DM, PH, PW and AGB, aligning with the observations from a previous study (39). The harvest index reflects the efficiency of assimilate translocation to the seeds, which play a vital role in crop yield. The negative correlation of HI with DM and AGB shows reduced allocation to reproductive organs in vegetative plants that mature later. As a result, a decrease in the efficiency of assimilate partitioning occurs, which reduces the value of HI. Additionally, delayed maturity increases maintenance respiration and allows the crop to reach terminal conditions that prevent grain filling, including heat or drought. Moreover, lodging and shade caused by dense, tall canopies may lower photosynthetic efficiency and assimilate flow to seeds. A study highlighted that increased inter-plant competition in late-maturing crops can exacerbate these effects by further limiting resource allocation to grain (46). Thus, although greater biomass may indicate vigorous growth, it does not ensure higher HI unless paired with effective partitioning.

Path coefficient analysis

Simple correlations may not fully capture the impact of individual traits on yield (39). Since multiple traits influence seed yield, path analysis is essential to determine the direct and indirect effects on yield. This approach helps develop a selection index to improve the effectiveness of breeding programs. The phenotypic and genotypic path coefficient analysis conducted in the present study showed that PW and AGB had the highest positive direct effect on YPP, supporting the positive correlation between them (Table 5). This implies that the increase of PW and AGB directly enhances YPP without the mediation of other traits. The higher path coefficient values indicate the strength of these relationships, suggesting that yield improvement in quinoa is possible through the direct selection of these two traits. Biologically, heavier panicles indicate a stronger sink capacity, allowing more assimilates to be directed and stored in the reproductive organs. Similarly, greater biomass production reflects a higher photosynthetic capacity and an improved ability of the plant to capture and utilise resources for growth, which are in compliance with previous research findings (39, 47). Conversely, TSW had a negative direct effect on YPP, indicating that selecting genotypes with lower TSW could increase YPP (39). Interestingly, HI exhibited a strong positive direct effect on YPP but showed a non-significant negative correlation with it. This discrepancy is likely due to HI's substantial negative indirect effect on AGB, a trait that positively influences YPP. The residual values were calculated as 0.0097 for the phenotypic level and 0.0078 for the genotypic level (Table 5). The very low residual value infers that most of the major factors responsible for variation were included in this experiment.

Genetic diversity studies

Cluster analysis groups genotypes based on trait similarities, offering insights into genetic and phenotypic diversity for breeding and conservation. In the present study, 46 quinoa genotypes were classified into 4 clusters based on D^2 values using Toucher's method, with each cluster sharing common traits. Similar clustering patterns were reported in another study, for 78 quinoa genotypes (48). The hierarchical dendrogram (Fig. 1) shows 4 clusters of quinoa genotypes. Cluster II was the largest (20 genotypes) and cluster III was the smallest (4 genotypes). Clusters II and III were characterised with higher TSW and earlier maturity. These traits are particularly valuable for Bangladesh's short growing seasons and climatic variability. Short-duration production methods benefit from the efficiency and adaptability of these genotypes. On the other hand, cluster IV contained the tallest plants with the highest PW, AGB, HI and YPP, suggesting a high potential yield and suitability for use as grain and fodder. They hold promises for integrated crop-livestock systems, promoting sustainable agriculture, due to their dual-purpose character. These findings align with a previous study which highlighted quinoa's potential as a dual-purpose crop for grain and livestock feed in Israel and Mediterranean countries (49).

In the present study, the average inter-cluster distances were higher than the average intra-cluster distances, indicating a greater degree of genetic diversity among the genotypes (Fig. 2), consistent with the findings in another research (50) . The largest inter-cluster distance was between clusters III and IV, suggesting substantial divergence, while the smallest was between clusters I and II, indicating close genetic relationships. The value of inter-cluster distance is important in hybridisation programs, as the extent of heterosis (hybrid vigour) largely depends on the degree of genetic diversity between the parental lines. Genetic divergence between clusters reflects variations in trait expression and allelic combinations. Because of the broad

genetic base, crossing genotypes from highly divergent clusters (like III and IV) enhances the chance of advantageous gene interactions, which can result in heterosis or hybrid vigour and result in better yields and adaptability and greater stress tolerance. On the other hand, genotypes that belong to the same cluster or closely related clusters, have fewer unique gene combinations because they share greater genetic similarities. As a result, hybridisation among them often leads to minimal improvement, since the scope for expressing beneficial non-additive effects is limited (51). Therefore crossing genotypes from clusters III and IV is expected to produce superior hybrids with complementary gene effects, leading to high-yielding varieties through recurrent selection (52).

Principal component analysis

Principal component analysis (PCA) reduces the complexity of data by identifying key traits contributing to overall variation. It is an important tool for guiding parental selection and breeding strategies. The first 2 components were considered the primary principal components due to their eigen values being higher than 1, which explain 73.97 % of the total variation (Table 8). Prior to this, the first 4 components were reported significant (Eigen value > 1) variability in the quinoa accessions (53). The first component, explaining 55.10 % of the variance, primarily reflected the significance of biological yield, including traits like AGB, PW and YPP. In contrast, the second component (18.87 %) emphasises commercial yield, with a focus on TSW and HI (Table 8). A previous study found that 58 % of the observed phenotypic variation is explained by the first two components (48). The identification of key traits contributing to variation through PCA provides valuable insights for breeding programs in Bangladesh, where traits linked to biological yield (AGB, PW, YPP) and commercial yield (TSW, HI) must be balanced to maximise productivity within short growing seasons. Enhancing biomass and PW, for example, can raise expected yield, while maximising seed size and HI promotes grain quality and economic benefits. By creating four separate groups, the PCA biplot diagram (Fig. 3) illustrated the diversity and distribution of both variables and genotypes. The most divergent genotypes were found to be Kaust-05784, Kaust-09391, Kaust-10860 and SAU Quinoa-1, according to the biplot. These genotypes can serve as donor parents in hybridisation programs to achieve greater hybrid vigour. Similarly, a previous study identified Quinoa Real, Amarilla de Maranganí and Quinoa Peruna as the most divergent genotypes among 30 studied genotypes (48). PCA helps with initial selection, but to verify these genotypes' stability in Bangladesh's unique agroclimatic conditions, multi-environment evaluation is necessary.

This study has some limitations, as the evaluation was carried out in a single environment and growing season, which may limit the generalisability of the results. Genotype × environment interactions were not examined. Therefore, further multi-location and multi-season studies are needed to validate these findings.

Conclusion

There is significant genetic variation for yield-related variables among the 46 quinoa genotypes studied, indicating a strong potential for yield improvement through selection and hybridisation. The traits PW, AGB and YPP exhibited high GCV and PCV coupled with high heritability and genetic advance, suggesting the predominance of additive gene action and the suitability of these traits for simple selection. To increase the production of quinoa, YPP should be given more priority which is strongly positively correlated with DM, PH, PW and AGB. The genotypes in cluster III (Kaust-09755, Kaust-10860, Kaust-09386, Kaust-09385, Kaust-10810, Kaust-09379 and Kaust-10804) were the most promising, based on yield and yield attributing traits which can be used for direct selection. Kaust-05784, Kaust-09391, Kaust-10860 and SAU Quinoa-1 showed the greatest divergence and could be used as parent materials in hybridisation programs for future improvement. Overall, these findings provide important insights to support efficient quinoa breeding and genetic improvement.

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Authors' contributions

SA and MAH conceived the idea of the study and developed the methodology. SA, BD and AA carried out the experiment and collected data. SA, BD and FAA performed data analysis. SA prepared the first draft of the manuscript. NS, MMR, DJB and MAH contributed to writing, review and editing. MMR and MAH supervised the work. All authors read and approved the final version of the manuscript.

Compliance with ethical standards

Conflict of interest: The authors do not have any conflict of interest to declare.

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