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Morphological traits of jackfruit (*Artocarpus heterophyllus* Lam.): Indicators of diversity, selection and germplasm dispersion in Uganda

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ABSTRACT

Uganda is one of the African countries with increasing production demands of jackfruit since it has gained popularity as a food and nutrition security crop with therapeutic benefits. However, the jackfruit germplasm in Uganda had not been adequately characterized to guide its production and there were reports of farmer-selection against inferior varieties. Therefore, this study comprehensively catalogued the morphological diversity of jackfruit to foster purpose-driven cultivation of jackfruit in Uganda; identified varieties and traits prone to negative selection to guide germplasm conservation efforts and established germplasm dispersion patterns to inform exchange programs of germplasm found suitable for commercial production. This was achieved using 47 qualitative and 30 quantitative traits of 249 jackfruit trees from four ethno-varieties, three administrative regions and three agro-ecological zones analyzed for the Shannon index (H'), coefficient of variation (CV), heritability (H^2), and genetic advance as percentage of the mean (GAM). Seed surface color was the most variable qualitative trait (H' = 3.16) and number of fruits per tree ($H^2 = 99.83$) and fruit weight (GCV = 69.45, PCV = 69.76) were the most diverse quantitative traits. Ethno-varieties of low economic value registered low diversity (Serebere: H' = 0.92, Namata: H' = 1.04), depicting negative selection against undesired varieties. The qualitative morphological diversity of jackfruit was highest in the Central region (H' = 1.07) and lowest in Eastern Uganda (H' = 1.02). Given the positive correlation between tree age and trunk circumference ($r = 0.99$, $p = 0.001$), the Central region with the oldest trees, largest trunks and samples with associations in Eastern and Western regions, is presumed the center of jackfruit diversity and pioneer of jackfruit cultivation in Uganda. In conclusion, jackfruit diversity in Uganda is still robust despite selection constraints. However, for future jackfruit improvements, it is vital to conserve the less preferred ethno-varieties.

Introduction

A jackfruit tree is a climatic and commercially valuable plant [7,24,51]. Its importance stems primarily from its large tree-borne

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fruits, which can measure up to 90 cm in length, 50 cm in width, and weigh up to 50 kg [7,32]. The fruits are used as food and raw material for value addition, yielding a variety of products such as cakes, biscuits, sweets, and ice cream. Jackfruit is widely regarded as an underutilized crop around the world [25,39]. However, due its nutraceutical properties, jackfruit has gradually gained popularity, particularly among patients suffering from HIV, high blood pressure, diabetes, and ulcers [39], all of which are still prevalent in Uganda and other parts of the world [30,42]. As such, there is increased demand for jackfruit in Uganda with many farmers opting for jackfruit cultivation as a cash crop, although, currently there are no large-scale monoculture jackfruit farms. Intercropping with bananas and coffee is common (personal observation). However, the jackfruit germplasm in Uganda had not been adequately characterized to guide farmers on the varieties suitable for commercial production. Moreover, market-driven demand for specific attributes of jackfruit [32,49], was exposing some varieties to negative selection pressure as farmers had started cutting down jackfruit trees whose fruits did not possess the attributes desired on the market (Nakintu et al., 2023). This was detrimental to the jackfruit's genetic diversity in Uganda, as it could be lost before documentation. Furthermore, the impacts of farmer-led selection on the diversity of jackfruit was underrepresented in the literature. Hence, this study was necessary to uncover the jackfruit germplasm threatened by farmer-led selection and its impacts on the diversity and distribution of jackfruit varieties in order to inform their conservation programs and future crop improvement strategies.

The rainforests of India's Western Ghats and Malaysia stand out as the likely origins of jackfruit. Given its edaphoclimatic adaptability, the crop spread from the Asian continent to other tropical and subtropical regions where it is a source of livelihood (Haq, 2006). Jackfruit's presence in Uganda is attributed to the Asians who came to Uganda in the 1890s to build the Uganda railway line and later for trade [10]. These Asians primarily settled in Uganda's commercial towns such as Kampala and Jinja, where it is assumed that they introduced jackfruit [21]. However, it was unknown how the jackfruit species spread into the country's current geographical range. Therefore, the current study assessed the morphological traits of jackfruit and traced the dispersion patterns of its germplasm from centers of diversity in Uganda.

Morphological characterization is based on an organism's observable qualitative and quantitative characteristics [31,54]. Morphological analysis is vital to agronomists and farmers for identifying and selecting fundamental traits present in a germplasm collection [9]. For instance, morphological variation allows farmers to select cultivars suitable for different agro-ecological zones. Morphological analysis also reveals the extent of the crop's diversity, history, trait plasticity (Guilherme Pereira and Des Marais; Sultan [14,45]), and transferability through the phenotypic coefficient of variation (PCV), genotypic coefficient of variation (GCV), heritability (H^2), and genetic advance (GA) ([54]; Ogunniyan & Olakojo, 2015). For instance, higher PCV than GCV values indicate environmental influence on a characteristic [19]. Similarly, heritability and genetic advance provide insights on transferability of a crop's quantitative traits, thus influencing the breeding and crop improvement strategies (Ogunningyan & Olakoyo, 2015; [19]; Kaur et al., 2018). Due to these benefits, morphological traits have been used to document the diversity of jackfruit and to select its germplasm. Sidhu [43], for example, reported a wide range of variation in morpho-agronomic characters of jackfruit attributed to cross-pollination and seed propagation. Disparities in jackfruit tree growth habits, canopy structure, leaf size, fruit shape, size, color, fruit-bearing (age and seasonality), maturity, density, size and shape of spines on the rind, sensory quality, flesh types, flavor, and taste have been observed [5,6,8,35,38,43]. Furthermore, morphological analysis has been used to identify superior jackfruit genotypes [5,43]. Rai et al. [38], for example, used morphological data to assess the yield and quality attributes of jackfruit grown in Eastern India. Similarly, Chandrashekar et al. [8] evaluated the performance of jackfruit grown in a coffee system, while Aswini et al. [5] used morphological data to identify popular varieties for commercialization.

Although such studies have been common especially in Asian countries (Haq 2006; [41]) and have revealed wide morphological variations, only one study had been conducted in Uganda covering two districts in the Central region [13]. Due to the wide morphological variation in jackfruit, coupled with the various environmental conditions under which it is grown [48], comprehensive regional studies with wider coverage of environmental variations were necessary to generate adequate information to guide production and commercialization of jackfruit in Uganda and Africa at large. Therefore, this study a) determined morphological variations among jackfruit varieties grown in three administrative regions and three agroecological zones of Uganda, b) established jackfruit varieties and traits under negative farmer-selection and c) traced the dispersion of jackfruit germplasm from centers of diversity in the country. The findings of this study provide direction to the production of jackfruit, enhancing food production, thus contributing to the attainment of Sustainable Development Goal 2 (SDG2) which focusses on ending hunger, achieving food security and promoting sustainable agriculture by 2030 and goal 5 of the African Unions' Agenda 2063. Sustainable production and commercialization of jackfruit, generate employment opportunities for the value chain actors contributing to poverty alleviation and realization of SDG1 and Goal 1 of the African Unions' Agenda 2063. Given its nutritive and therapeutic properties, increased production of jackfruit enhances its availability and consumption contributing to the attainment of SDG 4 and Goal 3 of the African Unions' Agenda 2063 which advocate for good health and proper feeding [3,47]. Information generated on selection against inferior jackfruit germplasm guides conservation strategies and aligns with SDG15 which looks out for life on land [47].

Materials and methods

Field work

Morphological variation among 249 mature jackfruit plants from 12 districts (Pallisa, Kamuli, Kayunga, Luweero, Iganga, Jinja, Mityana, Masaka, Mubende, Sembabule, Ibanda and Mbarara) belonging to three administrative regions of Uganda (Central, Eastern and Western) and three agro-ecological zones [Lake Victoria Crescent and Mbale Farmlands (LVCMF), Southern and Eastern Lake Kyoga Basin (SELKB) and Southwestern Grass Farmlands (SWGF)] [52], (Fig. 1) was assessed. Selection of sampling regions was based on results of the pilot survey conducted among traders in four major towns of Uganda (Kampala in the Central region, Jinja in the East, Mbarara in the Western region and Gulu in Northern Uganda). Out of the 42 traders interviewed in the pilot survey, 52.4 % obtained jackfruit from Eastern region, 35.7 % from the Central, 11.9 % from the Western region and no trader reported obtaining jackfruit from the Northern region. Therefore, Northern Uganda was excluded from the final survey. Over 95 % of the districts from which the traders obtained jackfruits in the three regions belonged to three agroecological zones (LVCMF, SELKB and SWGF). Sampling of jackfruit trees was based on availability of the jackfruit ethno-varieties in the three agroecological zones. From LVCM, 82 trees were studied, 86 from SELKB and 81 from SWGF. The number of samples was not evenly distributed because some varieties notably Serebera and Namata were rare in some agroecological zones. In fact, Serebera was mainly found in SELKB agroecological zone while Namata was most common in LVCMF. On-farm morphological measurements and observations were made following jackfruit descriptors from the International Plant Genetic Resources Institute [18]. The trees of the same variety studied were at least 1.5 km apart to minimize incidences of inbreeding.

Ethno-varieties of jackfruit

The 249 jackfruit trees studied were chosen from four ethno-varieties which had been described by Nakintu et al. [33], based on farmers' descriptions of pulp color and flake texture (Fig. 2a). Namata (firm with white pulps, $N = 66$), b) Serebera (soft with pale yellow pulps, $N = 14$), c) Namusaayi (firm with red/orange pulps, $N = 69$), and d) Kanaanansi (firm with yellow pulps, $N = 100$). The numbers of samples from the four ethno-varieties were not the same due to scarcity of some varieties particularly Serebera. The number of samples was not corrected for the varieties so as to establish the effect of reduction in abundance of these jackfruit varieties on their diversity. In this study, an ethno-variety is a category of jackfruit trees identified by farmers of a particular ethnic group/tribe using a single name (modified from Gwali et al. [15,16]).

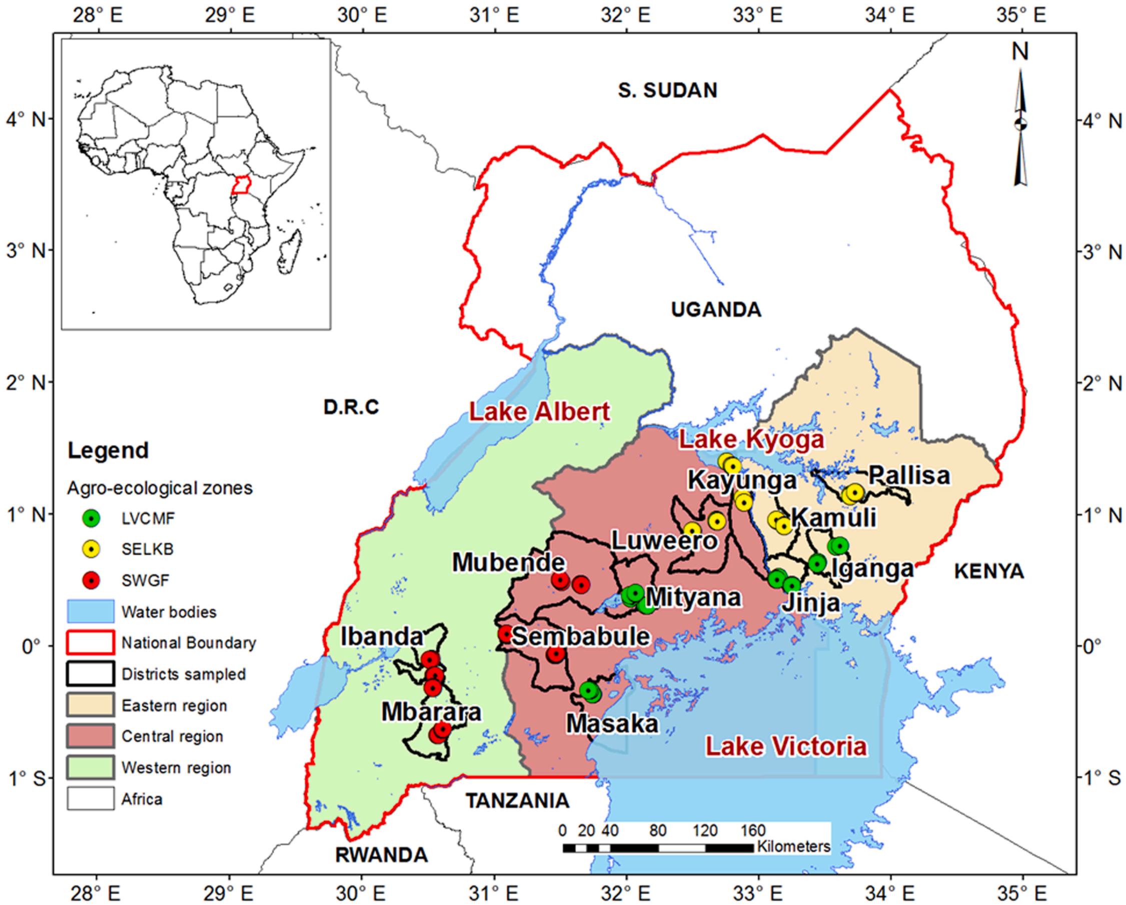

Fig. 1. A map of Africa showing the location of Uganda. Fig. 1b. Map of Uganda showing jackfruit sampling sites according to districts, agro-ecological zones, SELKB = Southern and Eastern Lake Kyoga Basin, LVCMF = Lake Victoria Crescent and Mbale Farmlands) and administrative regions (Central, Eastern, Western), created using ArcGIS version 10.4.

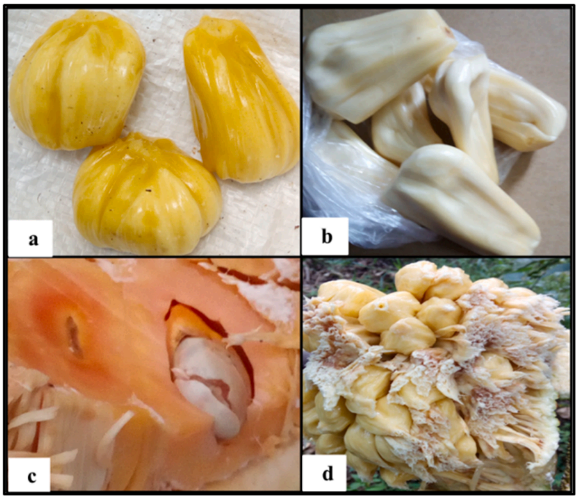

Fig. 2. Ethno-varieties of jackfruit trees studied. (a) Kanaananşi (b) Namata (c) Namusaayi (d) Serebera. Source: Field photos taken by Justine Nakintu between November 2018 and March 2019.

Data collection on morphological characteristics

Jackfruit descriptors included 47 qualitative characters (tree vigor, trunk surface, crown shape, tree growth habit, branching pattern, branching density, leaf blade shape, leaf apex shape, leaf base shape, leaf color, petiole shape, crotch angle of the petiole, leaf upper surface pubescence, leaf lower surface pubescence, midrib pubescence, female flower aroma, inflorescence color, secondary flowering, female inflorescence density, female inflorescence position, male inflorescence position, fruiting season, fruit-bearing habit, the beginning of the fruiting season, the end of the fruiting season, fruit-bearing position, fruit-clustering habit, fruit shape, fruit stalk attachment, fruit rind color, fruit rind surface, the shape of the spines, spine density, fruit attractiveness, latex exudation, flake shape, fruit texture, pulp color, pulp flavor/aroma, pulp juiciness, seed shape, seed coat sliminess, seed coat color, seed surface color, seed-to-

Table 1
Quantitative traits and their measurement methods.

SN	Trait	Method/Equipment used	Units
1	Tree height	Measuring tape	m
2	Trunk height	Measuring tape	m
3	Trunk circumference	Measuring tape	cm
4	Canopy diameter (East-West)	Measuring tape	m
5	Canopy diameter (North-South)	Measuring tape	m
6	Tree age	"Farmer reported"	years
7	Leaf blade length	Centimeter ruler	cm
8	Leaf blade width	Centimeter ruler	cm
9	Petiole length	Centimeter ruler	cm
10	Fruit stalk length	Centimeter ruler	cm
11	Fruit stalk diameter	Vernier calipers	mm
12	Fruit weight	Digital weighing scale	kg
13	Fruit length	Measuring tape	cm
14	Fruit diameter	Measuring tape	cm
15	Rind thickness	Vernier calipers	mm
16	Number of flakes/kg of fruit	Counting	counts
17	Weight of fresh flakes with seed per kg of fruit	Digital weighing scale	kg
18	Weight of fresh flakes without seed per kg of fruit	Digital weighing scale	kg
19	Flake/seed ratio	Calculated	NA
20	Flake length	Vernier calipers	mm
21	Flake width	Vernier calipers	mm
22	Flake thickness	Vernier calipers	mm
23	Flake harness	Penetrometer	pa
24	Rachis length	Measuring tape	cm
25	Rachis diameter	Measuring tape	cm
26	Seed length	Vernier calipers	mm
27	Seed width	Vernier calipers	mm
28	Number of seeds per kg of fruit weight	Counting	counts
29	100 seed weight	Digital weighing scale	kg
30	Number of fruits per tree	Counting	counts

kernel adherence, and heart-shaped fruits). These characteristics were directly observed and studied using the descriptions provided in the jackfruit descriptors [18]. After training a panel of 10 local people from each sampling site, pulp taste was determined through sensory tasting by ticking one of the following tests for a sample: insipid, sour, bitter, and sweet. On the other hand, various methods were used to collect data on 30 quantitative traits as shown in Table 1.

Jackfruit tree ages were obtained by interviewing farmers to support the prediction of the region where jackfruit cultivation began among the three regions studied. It was also important to ascertain whether tree age had any effect (positive or negative) on the economic variables of jackfruit. To minimize the effect of management practices on quantitative traits, the jackfruit trees, studied had not received any management procedure except weeding.

Data analysis

Shannon diversity indices computed with PAST version 3.26 [17] were used to assess the diversity of qualitative morphological traits. To reduce the age effect during statistical analysis, data of each quantitative character from individual samples with different ages was pooled to the respective jackfruit ethno-variety and tested for homogeneity. Analysis of variance (ANOVA) was performed to evaluate the variations in jackfruit diversity indices and pooled quantitative morphological data among ethno-varieties, administrative regions, and agro-ecological zones. ANOVA was used because the data set was normally distributed after a Kolmogorov test and comparisons of variation were required for independent variables with more than two factors (three agro-ecological zones, three administrative regions and four jackfruit ethno-varieties). Pearson correlation coefficient was used to obtain the best combinations of quantitative traits of jackfruit to guide selection of superior varieties for commercialization. Pearson correlation coefficient analysis was done because the quantitative parameters were measured, their data was normally distributed without significant outliers. Principal component analysis (PCA) based on both qualitative and quantitative morphological traits was used to investigate the relationship among jackfruit samples obtained from different administrative regions of Uganda. PCA was chosen for this data set because several quantitative traits had correlation coefficients greater than 0.3 [29] and it is suitable for displaying related variables. Upon fulfillment of test assumptions, ANOVA and correlation analysis were run in SPSS software version 20 [50], while principal component analysis was executed in R software version 1.1.463. (R [37]). Variability parameters (GCV, PCV, heritability (H^2), and genetic advance as percentage of the mean (GAM) were computed to provide information on the genetic properties of the Ugandan jackfruit population upon which, breeding decisions could be based. Genetic variability components ($\delta^2 g$ = Genotypic variance, $\delta^2 p$ = Phenotypic variance and $\sigma 2\ e$ = environmental variance) were computed as described by Abebe et al. [2], considering agroecological zones and administrative regions as locations and number of jackfruit ethno-varieties as replicates. From these components, GCV and PCV were calculated using the formulae suggested by Singh & Chaudhary [44] as follows:

$$\textbf{Genotypic coefficient of variation},\ GCV = \frac{\sqrt{\delta^2 g}}{\chi} X\ 100$$

Where: $\delta^2 g$ = Genotypic variance

χ = Mean of the trait

$$\textbf{Phenotypic coefficient of variation},\ PCV = \frac{\sqrt{\delta^2 p}}{\chi} X\ 100$$

Where: $\delta^2 p$ = Phenotypic variance
χ = Mean of the trait.

Broad sense heritability (H^2) was calculated using the formula suggested by Falconer & Mackay, [11].

$$\textbf{Heritability},\ H^2 = \frac{\delta^2 g}{\delta^2 p} X\ 100$$

Where: $\delta^2 g$ = Genotypic variance
$\delta^2 p$ = Phenotypic variance

The expected genetic advance (GA) for the studied traits was estimated using the formula used by Abebe et al. [2].

$$\mathrm{GA}\ (\%) = kH^2 \delta p$$

Where: GA = Expected genetic advance
k = standardized selection differentiation at 5 % selection intensity ($k = 2.063$)
H^2 = broad sense heritability

δ_p = phenotypic standard deviation

Genetic advance as percentage of the mean was computed using the formula:

$$\text{GAM} = \frac{GA}{\chi} X\ 100$$

Where: GAM = Genetic advance as a percentage of the mean

GA = Expected genetic advance

χ = Mean of the trait

Results

Diversity of qualitative traits of jackfruit in Uganda

The qualitative morphological diversity of 249 Ugandan mature jackfruit samples determined using 45 traits revealed high polymorphism across all studied traits, with varying degrees of contribution to the overall morphological diversity, with the exception of upper leaf surface pubescence, which was monomorphic. The Shannon diversity index (H') values ranged from 0.00 to 1.91, with a mean of 0.99 (Table 2). Although some traits had extremely low diversity indices, the qualitative traits studied revealed moderate overall diversity among Ugandan jackfruits.

Diversity of qualitative leaf traits

Overall, leaf traits had low to moderate diversity indices, with leaf blade shape being the most diverse leaf trait (H' = 1.43), followed by leaf apex shape (H' = 1.33), and upper leaf surface pubescence being monomorphic (H' = 0.00), with all 249 trees having glabrous upper surfaces (Supplementary Table 1).

Diversity of qualitative flower traits

Flower traits, likewise, showed low to moderate diversity, with female inflorescence position being the most diverse (H' = 1.61), expressed in six descriptor states (Supplementary Table 2). Secondary flowering had the lowest diversity index (H' = 0.63) among flower traits, with the majority of the trees (67.07 %) experiencing secondary flowering (Supplementary Table 2) and most trees (61.04 %) had male flowers on tertiary branches (Supplementary Table 2).

Diversity of qualitative fruit traits

All the qualitative morphological fruit descriptors studied were polymorphic and more variable than leaf and flower traits. Among these traits, fruit bearing position had the highest diversity index (H' = 1.91), followed by fruit shape (H' = 1.38) and fruit rind color (H' = 1.38) (Supplementary Table 3). A few trees (8.03 %) produced poor-quality fruits (irregular fruit shape, more fibers than pulps, very soft texture, small pulps, sour, dull colored pulps, very slimy pulps, not attractive), while the majority of the jackfruit trees (77.1 %) produced good to excellent fruits (firm texture, medium sized to big pulps, more pulps than fibers, brightly colored pulps, sweet, not slimy and attractive to the eye). Some jackfruit trees (17.3 %) had fruits with low latex exudation. The jackfruit trees exhibited three fruiting regimes; early (January to April), mid-season (May to August), and late (September to December), with the highest proportion of trees (46.59 %) having ripe fruits in December, January, and February. Fruits were mostly produced in clusters (83.53 %), with a few trees (16.47 %) producing solitary fruits (Supplementary Table 3). Farmers primarily planted and cared for jackfruit trees with regular fruiting habit (96.4 %). In addition to the main fruit shape, some jackfruit trees (12.45 %) produced heart-shaped fruits (Supplementary Table 3).

Table 2
Shannon diversity indices of the 45 qualitative morphological traits among the 249 jackfruit trees studied.

SN	Trait	H'	SN	Trait	H'	SN	Trait	H'
1	Tree vigor	0.83	16	Female flower aroma	0.99	31	Fruit rind surface	0.39
2	Trunk surface	0.46	17	Inflorescence color	1.14	32	Shape of spine	0.90
3	Crown shape	1.55	18	Secondary flowering	0.63	33	Spine density	0.84
4	Tree growth habit	0.78	19	Female inflorescence density	1.07	34	Fruit attractiveness	1.18
5	Branching pattern	1.21	20	Female inflorescence position	1.61	35	Latex exudation	1.02
6	Leaf blade shape	1.43	21	Male inflorescence position	1.09	36	Heart shaped fruits	0.38
7	Leaf apex shape	1.33	22	Fruiting season	1.06	37	Pulp taste	0.38
8	Leaf base shape	1.28	23	Start of fruiting season	1.73	38	Flake shape	1.86
9	Leaf color	1.06	24	End of fruiting season	1.83	39	Flake texture	0.23
10	Petiole shape	0.56	25	Fruit bearing habit	0.23	40	Pulp color	1.02
11	Crotch angle of petiole	0.68	26	Fruit bearing position	1.91	41	Seed shape	1.68
12	Grooves on the petiole	0.13	27	Fruit clustering habit	0.46	42	Seed coat sliminess	0.89
13	Leaf upper surface pubescence	0.00	28	Fruit shape	1.43	43	Seed coat color	0.93
14	Leaf lower surface pubescence	1.03	29	Stalk attachment	0.92	44	Seed surface color	3.16
15	Midrib pubescence	1.03	30	Fruit ring color	1.38	45	Adherence of seed	0.87

Diversity of qualitative pulp and seed traits

The pulp and seed traits of the jackfruits studied registered considerable diversity, with flake shape expressed in seven states having the highest Shannon diversity index (H' = 1.86) followed by seed shape (H' = 1.68) with six expressions (Supplementary Table 4). Although pulp and seed traits registered considerable diversity, some traits, especially those deemed to be of importance to the farmer, for example flake texture (H' = 0.23) and pulp taste (H' = 0.38), registered some of the lowest Shannon diversity index values. Seed coats and surfaces had different shades of color ranging from cream to dark brown. The majority of the trees (65.87 %) (Supplementary Table 4) produced seeds that could easily be separated from their coats, and the rest were either intermediate or very difficult to remove.

Qualitative morphological variation among jackfruit ethno-varieties, administrative regions and agroecological zones

Qualitative morphological variation among jackfruit ethno-varieties

Shannon diversity index analysis of 249 jackfruit tree samples from four ethno-varieties revealed five traits (flake texture, pulp color, presence of heart shaped fruits, sour taste and presence of the groove on the petiole) of descriptive value of the jackfruit ethno-varieties studied. The other traits were generally shared among varieties, though qualitative morphological variation was greater between varieties (62.22 %, $n = 28$) than within varieties (30.78 %, $n = 17$). The ethno-varieties had varying diversity indices, with Kanaanansi having the highest (H' = 1.06) diversity index, followed by Namusaayi (H' = 1.05) and Serebera having the lowest (H' = 0.92), as shown in Supplementary Table 5. Some of the most important qualitative traits, such as the beginning and end of the fruiting season and pulp/flake shape, had high diversity indices, particularly in Kanaanansi and Namusaayi ethno-varieties. The Kanaanansi ethno-variety had the lowest possibility of alternate fruiting and thus the lowest Shannon diversity index for fruit-bearing habit.

Qualitative morphological variation among administrative regions

Qualitative morphological assessment of the 249 jackfruit trees revealed moderate overall diversity among the administrative regions, although, the Central region harbored the highest diversity (H' = 1.07) followed by the Western region (H' = 1.05) while the Eastern region registered the lowest diversity (H' = 1.02), Supplementary Table 9. Though with variations in diversity indices, all the traits were obtained from all administrative regions with the exception of fruit bearing habit for which, trees with alternate fruiting

Table 3
Range (minimum and maximum), mean, variability, heritability and genetic advance as percentage of the mean of the quantitative traits of the 249 jackfruit samples.

SN	Trait	Min	Max	Mean	GCV (%)	PCV (%)	H^2 (%)	GA (% mean)
1	Tree height (m)	3.80	18.40	11.03	23.33	23.62	97.60	47.56
2	Trunk height (m)	0.40	3.80	1.87	42.22	43.88	92.58	83.81
3	Tree age	7.00	47.00	25.03	NA	NA	NA	NA
4	Tree circumference (cm)	39.00	250.00	134.64	33.79	33.81	99.86	69.66
5	Crown diameter (N-S, m)	2.50	16.00	8.90	32.61	32.96	97.86	66.55
6	Crown diameter (E-W, m)	2.50	16.30	8.72	32.47	32.83	97.81	66.24
7	Leaf length (cm)	10.30	19.92	14.83	12.45	12.66	96.68	25.25
8	Leaf blade width (cm)	5.44	10.21	7.75	11.70	12.10	93.47	23.33
9	Petiole length (cm)	1.08	2.42	1.73	16.96	18.70	82.21	31.72
10	Fruit stalk length (cm)	11.50	48.00	27.53	28.43	28.55	99.20	58.42
11	Stalk diameter (cm)	1.00	3.30	2.09	21.65	23.12	87.73	41.84
12	Fruit length (cm)	26.60	67.00	46.79	18.39	18.46	99.27	37.81
13	Fruit diameter (cm)	12.00	30.50	20.88	17.34	17.49	98.28	35.46
14	Fruit weight (kg)	1.40	51.00	14.75	69.45	69.76	99.13	70.10
15	Rind thickness (mm)	7.50	25.27	15.44	24.72	24.93	98.37	50.58
16	Number of flakes/kg	6.00	51.00	24.79	41.54	41.67	99.39	85.44
17	WFFS (kg)	0.10	0.71	0.43	29.00	35.59	66.42	48.76
18	WFF (kg)	0.05	0.55	0.31	33.11	42.14	61.74	53.68
19	Flake/seed ratio	1.00	7.00	3.79	55.75	56.69	96.72	88.41
20	Flake length (cm)	2.95	7.73	5.38	19.24	19.82	94.23	38.53
21	Flake width (cm)	1.72	4.48	2.96	18.30	19.34	89.54	35.72
22	Flake thickness (mm)	1.44	7.43	4.02	31.83	32.61	95.28	64.10
23	Rachis length (cm)	15.00	52.00	30.84	26.30	26.40	99.22	54.04
24	Rachis diameter (cm)	2.60	11.00	7.04	25.61	26.05	96.61	51.92
25	Seed length (cm)	2.08	3.58	2.82	11.27	12.34	83.36	21.23
26	Seed width (cm)	1.11	2.20	1.70	12.36	14.11	76.80	22.35
27	Number of seeds /kg	6.00	49.00	24.39	42.72	42.85	99.40	87.87
28	100 seed weight (kg)	0.11	1.36	0.59	58.12	63.71	83.22	91.42
29	Flake hardness ($x10^5$ pa)	2.00	12.00	7.86	29.83	30.23	97.37	60.72
30	Number of fruits per tree	9.00	150.00	77.92	64.94	65.00	99.83	74.70

Key: Min: Minimum, Max: Maximum, GCV: Genotypic coefficient of variation, PCV: Phenotypic coefficient of variation, H^2: Heritability GAM: Genetic advance as percentage of the mean, WFFS: Weight of fresh flakes with seed per kg of fruit, WFF: Weight of fresh flakes without seed per kg of fruit weight, NA: Not applicable since tree age is not an inheritable characteristic.

Table 4
Pairwise correlation matrix between quantitative morphological traits.

	TH	TC	TA	NSD	EWD	PL	FSD	FL	FD	FW	RT
TC	.567**										
TA	.564**	.999**									
NSD	.342**	.687**	.687**								
EWD	.386**	.703**	.703**	.803**							
PL	.153*	.140*	.141*	.159*	.148*						
FSD	−0.031	.015	.016	.003	−0.043	−0.022					
FL	−0.035	.039	.040	.103	.031	.104	.401**				
FD	.127*	.149*	.150*	.108	.094	.200**	.444**	.571**			
FW	.063	.068	.070	.154*	.109	.085	.348**	.600**	.648**		
RT	.055	.101	.101	.175**	.174**	.237**	−0.046	.123	.108	.042	
NF	−0.048	−0.057	−0.059	−0.154*	−0.141*	−0.092	−0.012	−0.086	−0.029	−0.289**	−0.276**
WFFS	−0.063	−0.051	−0.052	−0.040	−0.019	−0.054	.135*	.174**	.333**	.241**	−0.385**
WFF	.002	.028	.027	.017	.058	−0.042	.163**	.167**	.346**	.264**	−0.324**
FSR	.046	.063	.063	−0.006	.045	−0.060	.063	.071	.071	.122	−0.035
FLL	−0.003	.077	.078	.119	.123	.174**	.246**	.319**	.612**	.462**	.075
FLW	.084	.070	.073	.096	.107	.097	−0.033	−0.006	−0.022	.061	.100
FLT	−0.057	.014	.018	.032	.042	.091	−0.074	−0.032	−0.040	−0.001	.139*
RL	−0.005	.058	.058	.150*	.035	.127*	.322**	.748**	.530**	.582**	.115
RD	.059	.095	.097	−0.018	.012	−0.001	.308**	.349**	.660**	.461**	−0.164**
SL	.029	.010	.009	.058	.039	.041	.102	.273**	.379**	.255**	.038
SW	.046	.020	.020	.090	.078	.109	−0.111	−0.008	−0.084	−0.050	.186**
NSF	−0.026	−0.056	−0.057	−0.079	−0.074	−0.076	−0.023	−0.068	−0.071	−0.161*	−0.126*
100SW	−0.072	−0.103	−0.105	.027	−0.019	.034	.074	.100	.162*	.333**	.029
FH	−0.032	.036	.037	.050	−0.016	.235**	−0.152*	.078	.127*	.084	.297**
NFT	.406**	.477**	.475**	.430**	.425**	.072	−0.255**	−0.201**	−0.152*	−0.109	.039

Key: TH: Tree height, TC: Trunk circumference, TA: Tree age, NSD: Crown diameter (North-South), EWD: Crown diameter (East – West), PL: Petiole length, FSD: Fruit stalk diameter, FL: Fruit length, FD: Fruit diameter, FW: Fruit weight, RT: Rind thickness, NF: Number of flakes/kg of fruit, WFFS: Weight of flakes with seed /kg of fruit, WFF: Weight of flakes without seed/kg of fruit, FSR: Flake /Seed ratio, FLL: Flake length, FLW: Flake width, FLT: Flake thickness, RL: Rachis length, RD: Rachis diameter, SL: Seed length, SW: Seed width, NS: Number of seeds per kg of fruit, 100SW: 100 seed weight, NFT: Number of fruits per tree, **. Correlation is significant at the 0.01 level (2-tailed). *. Correlation is significant at the 0.05 level (2-tailed).

were not encountered in the Eastern region. The regions particularly registered high diversity in the start and end of the fruiting seasons revealing availability of jackfruits in these regions at different times of the year.

Qualitative morphological diversity among agroecological zones

Among the agroecological zones studied, the Southwestern Grass Farmlands (SWGF) had the highest diversity (H' = 1.07), followed by the LVCMF (H' = 1.06), SELKB had the lowest qualitative morphological diversity of jackfruit ((H' = 0.99). All morphological traits except grooves on the petiole and upper leaf surface pubescence were polymorphic among the three agroecological zones. Upper leaf surface pubescence was monomorphic across the three zones while grooves on the petiole were monomorphic only in SELKB. Fruit bearing habit registered low variability across all agroecological zones and its lowest Shannon diversity index value was obtained in SELKB. The start and end of fruiting seasons were highly variable among the three studied zones with the LVCMF having trees with the highest variability at the start of the fruiting seasons (H' = 1.99) while the end was most variable in SWGF (H' = 2.03).

Estimation of quantitative morphological variation of jackfruit in uganda

Table 3 summarizes the descriptive statistics (minimum, maximum, and mean), coefficients of variation (genotypic (GCV) and phenotypic (PCV), heritability (H^2), and genetic advance as a percentage of the mean (GAM) for the quantitative traits studied. The quantitative traits exhibited high diversity, as evidenced by high PCV and GCV values (> 20 %) observed in 20 traits (more than 60 % of the quantitative traits studied). Fruit weight, number of flakes per kg of fruit, flake/seed ratio, 100 seed weight, number of seeds per kg of fruit, and number of fruits per tree were the most diverse traits with high coefficients of variation (PCV and GCV > 40 %), whereas all leaf related attributes, such as leaf blade width, leaf blade length, and petiole length, were the least diverse with low coefficients of variation (PCV and GCV < 20 %). PCV values were greater than GCV values for all traits studied except tree age, for which these indices were not applicable. Broad sense heritability (H^2) and genetic advance as a percentage of the mean (GAM) were generally high, ranging from 61.74 % to 99.86 % and 21.33 % to 91.42 %, respectively. Petiole length and flake hardness varied significantly across jackfruit populations, regardless of variety (Supplementary Table 6) or geographical source (administrative region or agro-ecological zone) of samples (Supplementary Tables 7 and 8).

NF	WFFS	WFF	FSR	FLL	FLW	FLT	RL	RD	SL	SW	NS	100SW	FH
.325**													
.207**	.848**												
−0.077	−0.034	.397**											
−0.177**	.325**	.368**	.113										
−0.545**	−0.075	.036	.096	.198**									
−0.403**	−0.091	.027	.146*	.197**	.703**								
−0.069	.215**	.175**	−0.015	.273**	.005	.039							
.097	.379**	.362**	.072	.332**	−0.090	−0.101	.365**						
−0.120	.313**	.266**	−0.060	.505**	.168**	−0.019	.174**	.252**					
−0.432**	−0.228**	−0.166**	−0.001	.061	.469**	.248**	−0.019	−0.081	.470**				
.422**	.125*	.071	−0.095	−0.100	−0.124	−0.168**	−0.059	.010	−0.087	−0.193**			
−0.414**	.281**	−0.039	−0.546**	.208**	.181**	.032	.142*	.094	.264**	.130*	−0.195**		
−0.032	−0.057	−0.026	.035	.054	.070	.110	.075	.019	.087	.121	−0.051	−0.018	
.032	−0.087	−0.070	−0.030	−0.126*	.007	−0.046	−0.111	−0.114	−0.118	−0.012	.091	−0.141*	−0.016

Quantitative morphological variation among ethno-varieties, administrative regions and agro ecological zones

Quantitative morphological variation among jackfruit ethno-varieties

Based on the results of the ANOVA of the 30 quantitative traits, only five traits (petiole length, number of flakes per kg of fruit, flake/seed ratio, 100 seed weight, and flake hardness) showed significant variations ($p < 0.05$) among the jackfruit ethno-varieties studied. Thus, quantitative fruit-related traits, like qualitative traits, were extremely important in classifying jackfruit, accounting for four of the five significantly different traits. Variations in other quantitative traits among ethno-varieties of jackfruit were also observed, though not statistically significant (Supplementary Table 6).

Quantitative morphological variation among administrative regions

Fourteen traits (46.7 %) of the 30 traits studied including tree age and trunk circumference, showed significant variation ($p < 0.05$) across administrative regions (Central, Eastern, and Western). Unlike among ethno-varieties, where the majority of the significantly different traits were fruit related, the significantly different traits for administrative regions covered multiple parts of the plant. The Central and Eastern regions had the highest levels of these characteristics, while the Western region had the lowest levels (Supplementary Table 7). For instance, the Central region had the tallest trees (mean height = 11.49 ± 0.02 m), largest trunk circumference (145 ± 0.02 cm), crown diameter (N-*S* = 9.48 m) and the highest number of fruits per tree (61.76 ± 3.19). On the other hand, the highest values of trunk height (2.12 ± 0.08 m), rind thickness 17.36 ± 0.01 mm), number of flakes per kg of fruit (25.52± 1.21), number of seeds per kg (25.29 ± 1.06) and flake hardness ($8.98 \pm 0.20 \times 10^5$ pa) were obtained in the Eastern region.

Quantitative morphological variation among agro-ecological zones

Samples from the three agro-ecological zones (LVCBF, SELKB, and SWGF) showed significant differences ($p < 0.05$) in 14 (46.7 %) of the 30 traits studied (Supplementary Table 8). Nine of the 14 traits with significant variations among agro-ecological zones were fruit-based. All quantitative leaf traits investigated (leaf blade length, $p < 0.01$; leaf blade width, $p = 0.01$; and petiole length, $p < 0.01$) significantly varied among agro-ecological zones. Tree age and trunk circumference did not differ significantly among agro-ecological zones.

Correlation between quantitative traits

Pearson correlation analysis of the 30 quantitative traits revealed significant associations between several characteristics (Table 4). For example, tree age positively correlated with trunk circumference ($r = 0.99$, $p < 0.01$) and crown diameter (NSD, $r = 0.69$, $p < 0.01$, EWD, $r = 0.70$, $p < 0.01$). The weight of the fruit significantly ($p < 0.01$) and positively correlated with fruit diameter ($r = 0.65$), fruit length ($r = 0.60$), rachis length ($r = 0.58$), flake length (edible portion, $r = 0.46$), rachis diameter ($r = 0.46$), 100 seed weight ($r = 0.33$), seed length ($r = 0.26$), and number of flakes per kg of fruit ($r = 0.24$). Similarly, the number of fruits on a tree significantly ($p < 0.01$) and positively correlated with trunk circumference ($r = 0.48$), tree age ($r = 0.48$), tree height ($r = 0.41$), and crown diameter

(East-West /North-South diameter) ($r = 0.40$) (Table 4). Furthermore, petiole length had significant positive relationships with flake hardness ($r = 0.24$, $p < 0.01$), rind thickness ($r = 0.24$, $p < 0.01$), and fruit diameter ($r = 0.20$, $p < 0.01$). The size of the flakes (flake length) had significant positive correlations with petiole length, fruit stalk diameter, fruit length, fruit diameter, and weight. Nonetheless, negative correlations were observed among several traits, for example, the number of flakes per kg of fruit was negatively correlated to seed weight, flake width, and flake thickness (r −0.40, $p < 0.01$).

Principal component analysis of qualitative and quantitative morphological traits

Principal component analysis produced 19 components explaining 83.24 % of the total variance. The first and second principal components were retained because their eigen values were greater than one and contributed the highest proportions to the cumulative variation. The correlations were significant ($p < 0.01$). The two principal components plotted, (Fig. 3) revealed intermixing of samples from different locations, with close relationships between samples from the Central and Eastern, Central and Western, but distant relationships between samples from the Eastern and Western regions. The samples were categorized into two clusters, which are separated by the first principal component, PC 1. (Fig. 3). Samples from the Eastern and Central regions dominate the positive side of PC1, while samples from the Central and Western regions are mainly on the negative side of the same component.

Discussion

Diversity and selection as revealed by morphological traits of jackfruit

Some of the qualitative morphological traits revealed relatively high diversity in this study (Table 2, Supplementary Tables 1, 2, 3, 4, 5). High diversity among Uganda jackfruits has also been reported using SSR markers [32], which could be attributed to cross pollination, seed propagation and environmental suitability modifications [51]. High diversity was particularly observed among fruiting patterns, female inflorescence density, fruit rind and pulp colors. This shows that farmers pay little attention to these traits or they do not form the basis of selection of germplasm for planting. However, some important morphological traits for farmers, such as pulp taste (H' = 0.38) and fruit /flake texture (H' = 0.23), demonstrated low morphological diversity with dominance of the desired attributes. Of the 249 jackfruit trees studied, 87 % had sweet fruits and only 32 % had sour fruits. This probably signifies selection against trees with sour fruits given that the sweet taste is desired among jackfruits. In terms of fruit/flake texture, 94.38 % of the jackfruit trees were of firm type. For consumption purposes of the fruit, flakes with firm texture are preferred to the soft ones while the soft type is more beneficial for industrial application [13]. Since industrial uptake of jackfruit in Uganda is limited, most of the jackfruit is produced for consumption as fresh fruit and undesirable traits in terms of consumption have been negatively affected by farmer selection practices. Brightly colored pulps are one of the major traits that attract jackfruit consumers. In this study therefore, 80.3 % of the jackfruit trees studied had bright colors (yellow, red, pink and orange) while the remaining proportion was composed of trees with white pulps. In all the studied administrative regions and agroecological zones, fruit bearing habit registered low diversity because farmers preferred trees with regular than those with alternate fruiting habit. Therefore, 96.4 % of trees studied were of regular fruiting pattern and only 3.6 % fruited alternately. For centuries, farmers have relied on morphological traits to discriminate and adopt crop varieties. Therefore, the skewness of traits towards important fruit qualities such as firm, sweet and brightly colored pulps may be suggestive of a narrow genetic base for these traits and probably a sign of existence of unidirectional selection [27] for specific traits resulting in uniform phenotypes [54].

The presence of secondary flowering in majority of the jackfruit trees studied (67.07 %), as well as the high diversity of the start of the fruiting season (H' = 1.71) and end of the fruiting season (H' = 1.88) (Supplementary Table 2), are critical in ensuring jackfruit supply throughout the year. Secondary flowering results, on the other hand, contradict the findings of Aswini et al. [5] and Phaomei &

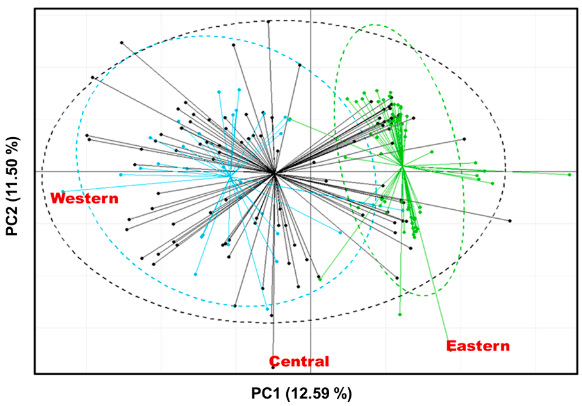

Fig. 3. Principal Component Analysis (PCA) for qualitative and quantitative morphological traits with individuals marked according to their origin (Western, Central and Eastern regions).

Mathew [35], who reported secondary flowering as a rare trait among Indian jackfruits. These findings could point to the existence of different genotypes in the two countries or the impact of environmental conditions on jackfruit phenology, hence, altering the fruiting patterns (Willis et al., 2008). For instance, the LVCMF agroecological zone had trees starting to fruit in all months of the year except April and July. In the SELKB, none of the trees studied started fruiting in months of March to July. Jackfruit trees studied in the SWGF were fruiting throughout the year except in September. These findings provide evidence on alteration of fruiting patterns of jackfruit trees by environmental conditions and in Uganda, conditions in the SWGF were the most favourable for jackfruit fruiting. Among the jackfruit ethno-varieties studied, Kanaanansi had fruits in all months of the year except June and July. Namata did not have fruits in April, July and November and the trees of Namusaayi were fruitless from April to June. Trees of the Serebera ethno-variety contained fruits for half a year (August to January) and the other months (February to July) had no fruits. These results suggest that as much as the environment may have a role to play, the genetic constitution of the variety is as well crucial in determining plant phenology regimes [40]. To exploit these fruiting patterns and to ensure availability of jackfruits for food security and regular market supplies, farmers should consider planting jackfruit trees of different varieties.

Morphological analysis also revealed that particular pulp colours (white, pale yellow, dark yellow, red and orange) and fruit textures (firm and soft) were definitive of the ethno-varieties. Additionally, heart-shaped fruits were only found on trees of firm varieties only, while other traits were widely shared among ethno-varieties (Supplementary Table 5). As a result, the two characteristics (pulp colours and fruit texture) are relied on to classify jackfruit into ethno-varieties, and heart-shaped fruits are promising morphological markers for distinguishing soft and firm varieties. These findings support the role of the fruit in shaping morphological variation in a variety of tropical trees, including *Tamarindus indica* L. [12], *Balanites aegyptiaca* L. [1], and *Vitellaria paradoxa* subsp. *Nilotica* [16]. It is clear that pulp color, fruit texture, and heart shaped fruits provide insights for identification and selection of superior jackfruit varieties suitable for commercial cultivation, although possession of heart shaped fruits requires further investigation.

The prolonged sharing of genetic material through outcrossing among jackfruit varieties in proximity locations (Supplementary Table 5) may account for the low phenotypic differentiation observed among the ethno-varieties studied. Since jackfruit is a perennial crop with a lifespan of about 80 years, individual trees share pollen repeatedly leading to production of highly related offspring with low genetic and phenotypic differentiation. Outcrossing has been reported among many long-living tropical trees ([1,16], Khan et al., 2010; [22]), jackfruit inclusive. Consequently, the ethno-varieties lose their distinctiveness. In support of this claim, the majority of the jackfruit trees (61.0 %) had their male inflorescence on tertiary branches. Chandrashekar et al. [8], reported similar findings in jackfruit trees in India. This could be an adaptation to promote pollen dispersal from one tree to another by wind since tertiary branches are small and weak, making them easily shaken by wind to disperse pollen to another tree in the vicinity regardless of the variety. These findings are consistent with molecular data from SSR analysis [32], which revealed little insignificant differentiation among ethno-varieties. Even at the molecular level, distinguishing jackfruit varieties remains difficult. For example, DNA barcoding based on the rbcL locus of soft and firm fruited trees failed to distinguish between the two varieties [22]. These results are similar to those obtained by Vazhacharickal et al. [48] in a phylogenetic analysis of six varieties of jackfruit from Kerala, India, using the matK gene, which revealed only one variable site. In addition, the low morphological diversity among varieties may be an indicator of selection by farmers. The traits may be highly heritable but selection by farmers may eliminate some variation leading to accumulation of uniform desired attributes among varieties of jackfruit.

Despite sharing most of the morphological traits, Kanaanansi and Namusaayi had higher genetic diversity (Supplementary Table 5), which could be attributed to their larger sample sizes compared to Namata and Serebera, which had fewer samples. Furthermore, these findings may reflect the impact of farmers' selection pressures on Namata and Serebera, whose morphological diversity was gradually declining. This type of selection, particularly against Serebera (the soft variety), has also been reported in Bangladesh (Khan et al., 2010), Malaysia [20], and India [39], highlighting the need for conservation efforts to save the jackfruit diversity, with a focus on the inferior varieties.

Quantitative morphological traits revealed a wide range of variation among jackfruit samples (Table 3). According to Kumar et al. [27], a coefficient of variation (CV) greater than 20 % indicates high variability, which was evident in this study, with 67.74 % of quantitative traits having GCV and PCV greater than 20 %. Quantitative variation was most pronounced among fruit related traits as evidenced by their GCV and PCV. This reinforces the significance of fruit-related traits as good differentiators among fruit crops [46, 54]. These findings are consistent with the findings of Phaomei et al. [36] in Indian jackfruit germplasm, where the number of fruits per tree and fruit weight had the highest coefficients of variation. This study found low diversity in leaf-related traits, which contradicts the findings of Phaomei and Mathew [35], who found high variability in leaf-related traitsof jackfruit in Indian which may be attributed to differences in jackfruit genotypes and environmental conditions that impact leaf traits differently. Nonetheless, petiole length varied significantly ($p < 0.05$) among ethno-varieties, with Namusaayi having the longest and Serebera having the shortest petiole (Supplementary Table 6). Although it is premature to use petiole length as a morphological marker, with further investigations especially at seedling level, it could be used in selecting jackfruit seedlings for planting.

The phenotypic coefficients of variation (PCV) of all quantitative traits studied were higher than their respective GCV (Table 2), indicating environment influence on the expressions of these traits [23,53]. Environment influence on the expressions of these traits is supported by results of PCA where jackfruit samples from the same origin were closely clustered. These findings are consistent with those obtained on the same samples through molecular analysis using SSR markers, which found significant correlations between environmental parameters (elevation, temperature, and precipitation) and genetic data [32]. Quantitative variability among jackfruit ethno-varieties was low, yet their heritability was high probably due to outcrossing, which has been reported in jackfruit by several authors including Lina & Protacio [28] and Obayashi et al. (2013). This implies that these traits are highly transmissible and with outcrossing, their genes are greatly shared among varieties leading to loss of variety-individuality and hence attaining high degrees of resemblance. Furthermore, GAM for all quantitative traits was high (> 20 %); portraying polygenic inheritance and additive gene action [4,19]. Therefore, selection rather hybridization is more beneficial in jackfruit improvement programs as the latter is unlikely to produce individuals with desired traits given that the generated hybrid may possess unwanted outcrossed genes from the parent plants.

Dispersion of jackfruit germplasm in uganda

Principal component analysis revealed intermixing of samples from the three administrative regions (Fig. 3), confirming that the crop was introduced because it showed low specificity to the location of sample collection [34]. According to Uganda's history, jackfruit was introduced by Asians [10] who primarily inhabited the Central region (Kampala) and Eastern region (Jinja) (Okoth, 1971); pointing to the probable areas where jackfruit should have been introduced in the country. Accordingly, correlation analysis revealed strong positive relationship between jackfruit tree trunk circumference and age (Table 4) and the Central region had jackfruit trees with the largest trunk circumferences followed by those from the Eastern and then the Western. Thus, the Central region should have adopted jackfruit cultivation first and other regions followed. Furthermore, the principal component output showed tight associations between samples from the Central region and samples from either administrative region (Eastern and Western), denoting the Central region as the center of jackfruit germplasm diversity in Uganda from which, the crop dispersed to other administrative regions within the country.

Morphological characteristics of biological and economic importance

The jackfruit samples examined revealed the presence of distinct characteristics among ethno-varieties of economic importance. In fact, Namata and Serebera, which were considered inferior varieties on the Ugandan market [33], demonstrated good traits that can be used to improve jackfruit germplasm. For example, Namata trees were the shortest (Average tree height = 10.8 m) hence, convenient for harvesting and also produced the largest fruits (fruit length = 47.9 cm, width = 21.6 cm). The Serebera ethno-variety trees had the largest trunk circumference (146.6 cm) and therefore produced the highest number fruits per tree (66) with soft and juicy flakes (Supplementary Table 6). Although fresh fruits from these two varieties have low consumer acceptability and economic value, the good traits they possess can be used to improve varieties with market desired characteristics. If jackfruit is adopted as an industrial crop, the two varieties could come in handy as raw materials since their productivity in terms of number of fruits per tree and size of fruits is greater than that of the superior varieties (Kanaanansi and Namusaayi).

The pulp/flake is the most important part of the ripe jackfruit [38], and the superiority of any genotype is dependent on the quality of the flakes. Of the four jackfruit ethno-varieties studied, Namusaayi had the highest flake/seed ratio (3.8), the firmest flakes (8.4×10^5 pa), and the biggest flakes (Flake length = 5.5 cm, flake width = 3.1 cm, flake thickness = 4.3 mm) which are brightly colored (Red). Hence, the Namusaayi ethno-variety falls into the category of superior genotypes. Furthermore, the thickness of its rind (15.8 mm) and hardness of its flakes (8.4×10^5 pa), reduce its perishability, allowing for easier transportation with less impact on shelf life, making it suitable for commercial purposes. As a matter of fact, it is essential to multiply the Namusaayi germplasm for interested farmers to plant.

Positive correlations between fruit quality traits such as fruit weight and flake length, number of fruits and trunk circumference (Table 4) are biologically and economically significant and may influence selection strategies. If the number of fruits a tree can bear can be estimated from its size (trunk circumference, tree height, and crown diameter), farmers and breeders can easily select superior planting materials.

Likewise, determining the size of flakes from petiole length, fruit stalk diameter, fruit length, diameter, and weight without cutting the fruit is essential for ensuring long shelf lives of the jackfruits given that traders would always make a cut on the fruit to ascertain the size of the flakes. Similar findings of positive correlation between fruit weight and pulp size were also reported for date palms [26].

Conclusions

Morphological trait analysis involving 249 jackfruit trees revealed considerable variation suitable for selection of superior germplasm for commercialization and also for future crop improvement. Since GAM results depicted polygenic inheritance of quantitative traits of jackfruit, its improvement programs should rely primarily on selection rather than hybridization.

Morphological traits were more diverse in superior ethno-varieties of jackfruit (Kanaanansi and Namusaayi) than inferior varieties (Namata and Serebera), confirming the existence of selection against less desirable jackfruit varieties. Although the variations may be due to the small sample sizes of the inferior varieties, these small numbers are key indicators of the negative consequences of selection to the genetic resource of these varieties that may be lost if appropriate conservation interventions are not devised. Therefore, inferior jackfruit varieties can be conserved in living gene banks. Alternatively, value addition avenues using these varieties as raw materials could be embraced so that farmers realize their benefits and get motivated to plant and conserve them in their fields.

Petiole length and heart-shaped fruits are promising morphological markers for discerning jackfruit varieties and selecting germplasm but require more research. Currently, identification and selection of superior varieties of jackfruit for fresh fruit consumptive commercial use is based on color, taste and texture of the pulp. As such, the brightly colored, sweet and firm pulps of Namusaayi and Kanaanansi make these varieties suitable for fresh fruit consumptive commercialization. Namata and Serebera, lacking in the fresh fruit consumptive traits are suitable for industrial product development.

The Central region was the first to adopt jackfruit cultivation and remains the center of jackfruit diversity in Uganda from which, the crop radiates to other areas within the country.

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Credit authorship contribution statement

The authors confirm contribution to the paper as follows: study conception and design: Justine Nakintu, Morgan Andama, Christian Albrecht, Julius B. Lejju and Eunice A. Olet; data collection: Justine Nakintu; data analysis and interpretation of results; Justine Nakintu, Morgan Andama, Christian Albrecht, Julius B. Lejju and Eunice A. Olet, Raphael Wangalwa; draft manuscript preparation: Justine Nakintu. All authors reviewed the results and approved the final version of the article.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.sciaf.2023.e01900.

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