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Genetic diversity evaluation and selection methods of sweet potato hybrid F_1 population based on SSR markers and phenotypic detection

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Abstract

Sweet potato (*Ipomoea batatas* (L.) Lam.) is a vital global crop, with breeding focused on both high starch and high yield. Hybrid populations are crucial for genetic improvement, but research on sweet potato hybrid F_1 populations remains limited. To explore the genetic laws of important traits in hybrid progenies, this study investigates the genetic diversity and efficient selection methods of the hybrid F_1 population from crossing between Yushu No.12 (high starch content) and Luoxushu No.9 (high yield) using phenotypic detection and SSR markers. Coefficients of variation, genetic distances, and similarity coefficients results showed that the F_1 population has rich genetic diversity. The parents and F_1 progenies could be clustered into 4 and 6 categories based on phenotypic detection and SSR markers, respectively. The results of transgressive inheritance analysis and cluster analysis showed that the hybrid F_1 population of sweet potato was closer to the female parent and might exhibit matroclinous inheritance. Based on the principal component analysis (PCA) results, a comprehensive scoring model was developed to select superior progeny. Correlation analysis revealed a strong link ($r=0.6420$) between the hardness and starch content of storage root, suggesting hardness could be used for rapid screening high-starch materials. Mantel test showed SSR markers as more reliable for evaluating genetic diversity than phenotypic analysis. These findings uncover the genetic diversity information of sweet potato F_1 generation, and provide strategies for the rapid and accurate selection of hybrid progenies, and lay theoretical foundation for deciphering the genetic mechanisms of important traits in sweet potato.

Keywords Sweet potato, Hybrid F_1 population, Genetic diversity, Phenotypic trait, SSR

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Introduction

Sweet potato (*Ipomoea batatas* (L.) Lam.), which flowers annually or perennially, is a kind of herbaceous root plant of Convolvulaceae. As a vital global staple crop and important industrial material, which distinguished as its high yield, high starch content, nutritional value, and adaptability to various environmental conditions [1], sweet potato has been cultivated extensively in over 120 countries worldwide [2]. By 2022, the global sweet potato harvest area has reached 7,248,381 hectares [3].

Hybrid populations of sweet potato form the foundation for genetic improvement and breeding programs. Selecting superior breeding lines from the F_1 population in sexual reproduction has been a critical method in sweet potato breeding [4], essential for enhancing traits such as yield, disease resistance, and nutritional quality. Genetic diversity refers to the heritable variation within a species population, measuring genetic distance or similarity [5]. The lack of genetic diversity information in F_1 populations hinders the effective utilization of these populations in breeding programs aimed at enhancing crop adaptability and genetic improvement. Understanding the variation and segregation in sweet potato progenies is crucial for developing new varieties, and genetic improvement of important traits. However, sweet potato is a highly heterogeneous hexaploidy crop with a complex hybrid genetic background [6, 7] and diverse variation types. The F_1 progeny from hybridization exhibit high genetic variation, and the selection of parents and offspring is often blind and lacks foresight. Traditional methods only relying on phenotypic traits such as stem diameter, vine length, branch number, and yield may not sufficiently reflect the true segregation of F_1 populations and help with accurate selection of superior breeding lines. Therefore, there is an urgent need to evaluate the genetic diversity of sweet potato F_1 hybrids precisely and to develop more robust methods to identify superior lines, and thereby accelerating and promoting the genetic improvement of sweet potato.

Since its development in the late 1980s and early 1990s, Simple Sequence Repeat (SSR) molecular marker technology has become an ideal tool for assessing plant genetic diversity and identifying germplasm resources due to its high polymorphism and co-dominance [8]. It has been widely used in the genetic diversity studies of crops such as wheat [9], winged bean [10], mango [11], Chinese cabbage [12], and walnut [13]. In sweet potato research, Hu et al. [14] developed and identified microsatellite markers in sweet potato, laying the foundation for subsequent genetic diversity studies. Luo et al. [15] constructed a sweet potato germplasm fingerprint library, while Meng et al. [16] analyzed the sweet potato germplasm fingerprint map. Zhang et al. [17] used ISSR markers to study the genetic diversity and population structure of 240 sweet potato germplasm resources, finding that the genetic diversity of in the tested sweet potato germplasm collection in China was lower than that in some reported germplasm collections from other regions. It was found that combining phenotypic detection and SSR molecular marker technology could explore plant genetic diversity more comprehensively and optimize breeding strategies. For instance, Karuri et al. [18] utilized morphological traits and SSR markers to assess the high genetic diversity in sweet potato germplasm and found that both effectively distinguished different sweet potato genotypes. Li et al. [4] investigated the genetic diversity of a F_1 hybrid population using SSR markers and 13 agronomic traits, and found there were differences between cluster analysis results based on agronomic traits and SSR markers, and the variation of genetic distance detected based on agronomic traits were higher than that based on SSR markers. Palumbo et al. [19] combined morphological traits, quality traits, and SSR molecular markers to provides a more comprehensive study of sweet potato genetic diversity. To date, this integrated approach to analyzing genetic diversity has been widely applied to crops such as lima bean [20], rice [21], sesames [22], maize [23], and so on. However, most studies utilizing phenotypic detection and SSR molecular markers to evaluate genetic diversity have focused on germplasm resources, with limited research on the genetic diversity of hybrid populations. Although a few studies have explored the patterns of trait variation [24] and matroclinous inheritance [25] in the hybrid F_1 populations of sweet potato, none have proposed a more accurate method for selecting superior hybrid progeny.

In this study, we performed a hybridization between the high dry-content cultivar Yushu No.12 and the high-yield cultivar Luoxushu No.9. We analyzed yield, quality, and morphological traits of 303 individual plants from the F_1 hybrid population, incorporating SSR molecular markers into our analysis. This research investigates the genetic diversity of starch-type and high-yield sweet potato hybrid F_1 populations, providing theoretical and practical foundations for the early selection of new sweet potato varieties with both high dry matter and high yield. Additionally, the study inferred the genetic patterns of sweet potato hybrid traits, offering a rich theoretical basis for future sweet potato genetic improvement.

Materials and methods

The origin and characteristics of parents

The hybrid combinations were Yushu No.12 (female parent) and Luoxushu No.9 (male parent). The female parent, Yushu No.12, is a starch-type sweet potato cultivar developed by Southwest University. It is characterized by pink skin and light yellow flesh. It has exhibited the following traits over two years of field tests (2011 and

2012): average stem diameter of 0.6 cm, 3 basal branches, maximum vine length of 210 cm, a fresh yield of 25,500 kg·hm^{-2}, 4 storage roots per plant, with dry matter content of 36.42%, and the starch content of 25.33%. The male parent, Luoxushu No.9, is a dual-purpose sweet potato cultivar jointly developed by the Luohe Academy of Agricultural Sciences in Henan Province and the Xuzhou Sweet Potato Research Center in Jiangsu Province. It is characterized by red skin and light yellow flesh and has exhibited the following traits over two years of field evaluation: average stem diameter of 0.6 cm, 7–8 basal branches, maximum vine length of 190 cm, a fresh yield of 33,000 kg·hm^{-2},4.3 storage root per plant, the dry matter content was 31.15%, and the starch content was 20.74%. The photographs of the parents were shown in the supplementary material Figure S.1.

Cross breeding

The plant parents were hybridized at the southern breeding base of Southwest University in Lingshui County, Hainan Province. Mature seeds were harvested, aired, and preserved for later use.

Field cultivation

The harvested hybrid seeds germinated and were sown in the field. When the seedlings grew to approximately 20 cm, they were topped to promote branch growth. Two months later, 3 tip seedlings (around 25 cm) were cut from per branch to get 909 plants and transplanted in the Xiema base of Potato Crops Research Institute of Southwest University. The planting row spacing was 0.80 m, with a plant spacing of 0.21 m and a ridge width of 5 m. The planting density was 60,000 plants/hm^2. Protective rows around the experimental field were established, and other management practices followed conventional methods. Harvesting was conducted another five months later.

Determination of yield, quality, and morphological traits

According to the previous reported methods [26], measurements were conducted approximately 10 days before harvesting for each plant's stem diameter, number of basal branches, and maximum vine length. During harvesting time, the fresh yield and number of large and medium and small storage roots of a single plant were measured individually. Additionally, storage roots' average hardness and dry matter content were measured per plant, with subsequent calculations of starch content and yield per plant. For further analysis, measurement data were averaged from three sweet potato plants derived from the same seed (same number). Hardness was measured with the fruit hardness tester GY-4 (Zhejiang Tuopu Instrument Co., LTD.), with the highest pressure value (kg·cm^{-2}) recorded as the hardness value, the division value being 0.01 kg·cm^{-2}. Dry matter content was determined using the conventional drying method and calculated according to the method of Lv et al. [27]. Starch content was calculated according to the dry matter content conversion method of Wang et al. [28]. Starch yield per plant was calculated following the method of Yang et al. [29]. The calculation formulas are as follows:

Starch Content (X_{10}):

$$X_{10} = X_9 \times 0.86945 - 6.34587 \quad (1)$$

Where X_9 represents the dry matter content.

Starch Yield Per Plant (X_8):

$$X_8 = (X_4 + X_6) \times X_9 \quad (2)$$

Where X_4 represents the fresh yield of large and medium storage roots per plant, X_6 represents the fresh yield of small storage roots per plant, and X_{10} represents the starch content.

SSR marker detection

Genomic DNA extraction

Around 60 days after transplanting in the field, three leaves were collected from the plant derived from each seed, and the genomic DNA was extracted using the improved CTAB method [30]. The quality of the DNA was tested via 1% agarose gel electrophoresis, and the DNA concentration was tested using a NanoDrop One microvolume UV-Vis spectrophotometer (Thermo Fisher Scientific).

Primer selection

A total of 300 SSR primer pairs, which developed in our previous study [31], were preliminarily screened and selected from them. DNA from 22 randomly selected F_1 progeny and parental samples was used as the template for primer screening. Eighteen primer pairs were selected for further test due to their high amplification efficiency, high probability to produce clear DNA bands, high polymorphism, and good reproducibility when using these DNA of F_1 progeny as templates. The primers used in this study are listed in Supplementary material Table S.1.

PCR amplification

PCR amplification reaction system: 10×PCR buffer, 1 μL; $MgCl_2$, 0.4 μL (25 mmol·L^{-1}); DNA template (50 ng·μL^{-1}), 1 μL; Forward primer and Reverse primer, l μL (10 μmol·L^{-1}) each; dNTPs, 0.2 μL (10 mmoL·L^{-1}); Taq enzyme, 0.1 μL (5 U·μL^{-1}); add ddH_2O to 10 μL.

Reaction conditions: pre-denaturation at 94 ℃ for 5 min; denaturation at 94 ℃ for 45 s; renaturation at 55℃ for 45 s, extension at 72 ℃ for 1 min, 35 cycles; extension at 72 ℃ for 10 min.

PAGE gel electrophoresis and detection

PCR products were subjected to electrophoresis using a 6% non-denaturing polyacrylamide gel at 150 V and 100 A for 1 h. It was detected with silver staining, and the results were photographed and preserved [32].

Data processing

DPS 7.05 software was used to conduct statistical and principal component analyses of phenotypic traits. Correlation analysis and frequency distribution analysis for 11 phenotypic traits were conducted using Origin 2021 software, while skewness, kurtosis, and the one-sample Kolmogorov-Smirnov test were calculated using Excel 16.87 software. After SSR detection, the location of clear and legible electrophoretic bands was recorded with the "0–1" system and to create a 0–1 matrix for the SSR molecular markers of the samples. Genetic diversity indices (Simpson index and Shannon-Weaver index), genetic distances, and similarity coefficients for phenotypic data and SSR markers were calculated using RStudio 2024 software, which was then used to construct genetic distance matrices and perform clustering analysis. The *t*-test were calculated using RStudio 2024 software. Before calculating the diversity indices, the phenotypic traits were categorized based on the previous research method [33], with the mean ($\bar{x}$) as the baseline and 0.5 standard deviations (s) as the class interval. The smallest class included values less than $\bar{x} - 2s$, and the largest class included values greater than $\bar{x} + 2s$. The Unweighted Pair-Group Method with Arithmetic Means (UPGMA) method was employed for cluster analysis of phenotypic data, and the Neighbor-Joining (NJ) method was used for cluster analysis using SSR molecular marker detection data. The calculation formulas are as follows:

Simpson index (*S*):

$$S = 1 - \sum_{i=1}^{n} P_i^2 \tag{3}$$

Where P_i represents the proportion of samples in the i -th category relative to the total number of samples.

Shannon-Weaver index (*H'*):

$$H' = -\sum_{i=1}^{n} P_i \ln P_i \tag{4}$$

Where P_i represents the proportion of samples in the i -th category relative to the total number of samples.

Results

Genetic diversity analysis based on phenotypic traits

Phenotypic analysis of parental and hybrid F1 populations

Frequency distribution histograms were generated for 11 phenotypic traits of the hybrid F_1 population (Fig. 1). Most traits exhibited a frequency distribution pattern with a central peak and tapering at both ends. A one-sample Kolmogorov-Smirnov test indicated that the traits of maximum vine length, dry matter content, starch content, and hardness followed a normal distribution ($p > 0.05$). However, the remaining traits deviated from normality ($p < 0.05$), and except for the number of basal branches, the absolute values of kurtosis and skewness exceeded 1.00.

The statistical analysis of the main morphological traits, yield traits, and quality traits of the parents and hybrid F_1 population (Table 1) showed that the quality traits (dry matter content, starch content, and hardness) of the hybrid F_1 population were relatively stable, with coefficients of variation lower than 15%. The variation of yield traits (the fresh yield and number of large and medium storage roots per plant, the fresh yield and number of small storage roots per plant, and the starch yield per plant) were relatively high, with a variation coefficient higher than 80%. Morphological traits (stem diameter, number of basal branches, and maximum vine length) exhibited coefficients of variation ranging from 37.6–47.1%, which were relative medium. Based on the genetic diversity analysis, the Simpson Index (*S*) for the 11 phenotypic traits ranged from 0.6932 to 0.8569, with an average of 0.8063, while the Shannon-Weaver Index (*H'*) varied from 1.3093 to 2.0746, with a mean value of 1.8192. Among these indices, large and medium storage roots exhibited the lowest *S* (0.6932) and *H'* (1.3093) values, indicating relatively low genetic diversity for this trait. In contrast, quality traits (dry matter content, starch content, and hardness) showed the highest *S* values (0.8569, 0.8569, and 0.8536, respectively) and *H'* values (2.0746, 2.0746, and 2.0576, respectively), reflecting high levels of genetic diversity. Overall, the genetic diversity within the population is relatively high.

When considering both the hybrid parents and the F_1 population, quality traits showed higher average values in the female parent (Yushu No.12) than in the male parent (Luoxushu No.9). The F_1 population exhibited ratios exceeding 71% above the male parent and more than 58% above the mid-parent value for quality traits, with relatively high ratios also exceeding the female parent, indicating a significant maternal genetic influence on quality traits. For yield traits, average values were higher in the male parent than in the female parent. In the F_1 population, except for the fresh yield of small storage roots per plant, ratios more than the female parent and mid-parent values were not higher than 32%, and ratios more than

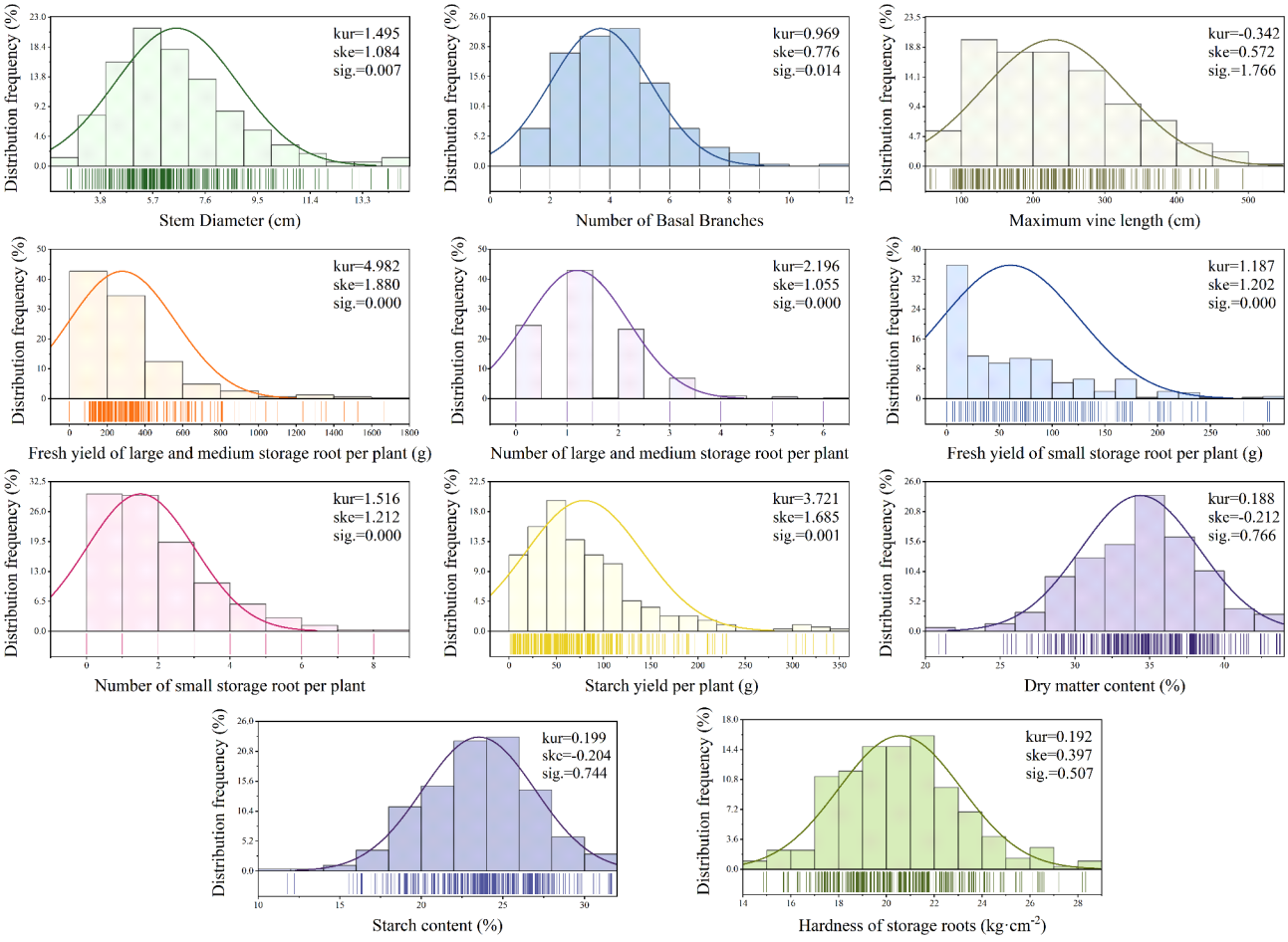

Fig. 1 Frequency distribution of 11 phenotypic traits
Kur, kurtosis; Ske, skewness; Sig., one-sample Kolmogorov-Smirnov significance value, which is equivalent to the *p*-value in this study. If Sig. (i.e., *p*) > 0.05, it means the trait is normally distributed

the male parent were lower than 22%, suggesting a significant maternal genetic influence on yield traits as well. As for morphological traits, there was little difference in average values for stem diameter and maximum vine length between the parents, while the average number of basal branches was significantly lower in the female parent than in the male parent. In the F_1 population, proportions more than the female parent, male parent, and mid-parent values were around 50% for stem diameter and maximum vine length. Proportions more than the male parent and mid-parent values were not higher than 12.5% for the number of basal branches, indicating that morphological traits may also primarily be influenced by maternal genetic factors.

PCA of main morphological traits, yield traits, and quality traits

The eigenvalues and the contribution rates of the principal components are the basis for selecting principal components, and the principal components are extracted according to the principle of the cumulative contribution rate greater than 85%. As shown in Table 2, the cumulative contribution rate of the first 5 principal components is 85.6063%, from which most information about the 11 traits has been reflected. Therefore, the first 5 principal components can be selected as comprehensive analysis indexes. Based on the normalized eigenvector values (Table 3), the functions for the 5 principal components were obtained and subsequently used in the construction of a comprehensive scoring model.

In the first principal component, the fresh yield of large and medium storage roots, the number of large and medium storage roots per plant, and the starch yield per plant had large positive coefficients of 0.5150, 0.4612, and 0.4669, respectively. This indicates that the first principal component mainly reflects the comprehensive index of the main yield traits of sweet potatoes and can be called the "main yield traits factor". In the second principal component, dry matter content, starch content, and hardness had positive coefficients of 0.5811, 0.5811, and 0.4921, respectively. This mainly reflects the quality traits of sweet potatoes and can be called the "main

Table 1 Statistical analysis on traits of parents and hybrid F_1 population in Yushu No.12×Luoxushu No.9 hybrid population

Traits	Parents			Hybrid F_1 population								
	FP	MP	PM	Max	Min	Mean	CV	MTFP (%)	MTMP (%)	MTP (%)	S	H′
Morphological traits												
X_1	0.6	0.6	0.6	1.47	0.26	0.66	37.6	46.9	46.9	46.9	0.8377	1.9644
X_2	3	7	5	11	1	3.7	47.1	51.2	2.6	12.5	0.8208	1.8468
X_3	210	176	192	520	56	228	43.2	54.1	63.7	57.4	0.8515	1.9931
Yield traits												
X_4	350	450	400	1666	0	280	102.8	28.4	17.5	22.8	0.7653	1.6172
X_5	1.6	2	1.8	6	0	1.2	82.9	32	8.9	32	0.6932	1.3093
X_6	35	75	55	306	0	63	123.9	54.1	35.3	44.2	0.7503	1.6419
X_7	2	2	2	8	0	1.5	100.1	21.8	21.8	21.8	0.7691	1.5900
X_8	97.52	108.88	103.2	343.61	0	79.87	80.7	28.7	21.8	26.1	0.8145	1.8420
Quality traits												
X_9	36.4	31.2	33.8	43.7	20.9	34.4	11.7	30.7	79.2	58.7	0.8569	2.0746
X_{10}	25.3	20.7	23	31.7	11.8	23.6	14.8	30.4	79.2	58.7	0.8569	2.0746
X_{11}	19.6	19	19.3	28.3	14.9	20.6	12.7	62.7	71.3	66.7	0.8536	2.0576

X_1-X_{11}: Stem diameter (cm), Number of basal branches, Maximum vine length (cm), Fresh yield of large and medium storage root per plant (g), Number of large and medium storage root per plant, Fresh yield of small storage root per plant (g), Number of small storage root per plant, Starch yield per plant (g), Dry matter content (%), Starch content (%), Hardness of storage roots ($kg{\cdot}cm^{-2}$), respectively. The same applies to Tables 3 and 4, and Fig. 3

FP: Female parent; MP: Male parent; PM: Pro median; Max: Maximum; Min: Minimum; CV: Coefficient of variation; MTFM: More than the proportion of female parent; MTMP: More than the proportion of male parent; MTP: More than the proportion of the mid-parent value; *S*: Simpson diversity index; *H′*: Shannon-Wiener index

Table 2 Eigenvalue, contribution rate, cumulative contribution rate

Principal component	Eigenvalue	Contribution (%)	Cumulative contribution (%)
1	3.1762	28.8745	28.8745
2	2.5808	23.4621	52.3365
3	1.8021	16.3829	68.7194
4	1.0592	9.6293	78.3488
5	0.7983	7.2576	85.6063
6	0.6212	5.6473	91.2537
7	0.4564	4.149	95.4027
8	0.3074	2.7949	98.1976
9	0.1795	1.6322	99.8298
10	0.0187	0.1697	99.9996
11	0	0.0004	100

Table 3 Normalized eigenvector values of 5 principal components

Principal component	Normalized eigenvector values										
	X_1	X_2	X_3	X_4	X_5	X_6	X_7	X_8	X_9	X_{10}	X_{11}
Y_1	0.2642	0.2703	0.2858	0.5150	0.4612	-0.1430	-0.1200	0.4669	-0.1370	-0.1370	-0.0840
Y_2	0.0388	-0.0420	-0.0590	0.1075	0.1078	-0.0610	-0.0880	0.2026	0.5811	0.5811	0.4921
Y_3	0.0401	0.1745	0.0678	0.0194	0.0374	0.6766	0.6801	0.1885	0.0315	0.0314	0.0607
Y_4	0.6856	0.6011	-0.1410	-0.1860	-0.2520	-0.0660	-0.0480	-0.1930	0.0571	0.0566	0.0047
Y_5	0.0176	0.0053	0.9343	-0.2190	-0.0810	-0.0760	0.0375	-0.2160	0.0840	0.0836	0.0655

quality traits factor". In the third principal component, the fresh yield and number of small storage roots per plant had, more significant positive coefficients of 0.6766 and 0.6801, respectively, reflecting the comprehensive index of small storage roots yield traits and can be called the "minor yield traits factor". In the fourth principal component, the stem diameter and the number of basal branches have more significant positive coefficients of 0.6856 and 0.6011, respectively. In the fifth principal component, maximum vine length has a significant positive coefficient of 0.9343. The fourth and fifth principal components mainly reflect the comprehensive index of the main morphological traits of sweet potato and can be called the "main morphological traits factor".

Using the proportion of each principal component's eigenvalue relative to the total eigenvalue sum of the extracted principal components as weights, the comprehensive scoring model for principal components can be calculated as:

$$F = 0.1860\ X_1 + 0.1811\ X_2 + 0.1566\ X_3 + 0.1674\ X_4 + 0.1571\ X_5 + 0.0507\ X_6 + 0.0633\ X_7 + 0.2091\ X_8 + 0.1326\ X_9 + 0.1325\ X_{10} + 0.1242\ X_{11}.$$

According to the comprehensive scoring model, the comprehensive score and ranking of the parents and 303 hybrids F_1 population can be calculated, as shown in Table 4 (parents and the top 20 of F_1). Among the 305 materials, No.61 of the hybrid F_1 population has the highest score of 397.77, ranked 1st, while No.33 of the hybrid F_1 population has the lowest score of 22.65, ranking 305th. The male parent ranked 76th with a score of 141.51, and the female parent ranked 106th with a score of 126.26. The photographs of the best F_1 hybrid, No.61 were shown in the supplementary material Figure S.2.

Box plots were created for 11 phenotypic traits, comparing the top 20 plants selected using the comprehensive scoring model with the other plants (Fig. 2). The results clearly illustrate that the selected plants exhibited significantly superior traits, particularly in terms of maximum vine length, the fresh yield and number of large and medium storage roots, and starch yield per plant, while producing lower fresh yield and number of small storage roots compared to the other plants. This analysis reveals that the top 20 selected plants exhibit advantages in morphological traits and yield traits, while showing no notable superiority in quality traits. This effectively identified high-yield sweet potato individuals, confirming that higher comprehensive scores correspond to better phenotypic traits, especially those related to yield. Furthermore, the comprehensive scoring model also enabled the assessment of each trait's relative importance and contribution within the plants.

Correlation analysis between the various traits of the hybrid F_1 population

Correlation analysis between some traits of the hybrid F_1 population (Fig. 3) showed that main aboveground morphologic traits (stem diameter, number of basal branches, maximum vine length) showed positive correlations with each other (correlation coefficient $r = 0.3747$, 0.1567, and 0.1769, respectively). Fresh yield and number of large and medium storage roots showed significant positive correlations with main aboveground morphological traits

Table 4 Comprehensive score of each factor and ranking of tested materials (parents and the top 20 of F_1)

No.	X_1	X_2	X_3	X_4	X_5	X_6	X_7	X_8	X_9	X_{10}	X_{11}	CS	*R*
61	1.10	8	264	1666	4	0	0	310.87	28.76	18.66	17.35	397.77	1
60	0.81	6	253	1526	5	56	2	343.61	32.28	21.72	19.49	382.81	2
300	0.96	4	520	1298	3	44	1	314.00	34.24	23.42	22.75	380.07	3
215	0.98	4	395	1332	6	282	5	303.69	28.94	18.82	17.39	374.90	4
283	0.63	7	292	1456	2	36	1	295.26	30.06	19.79	19.27	364.82	5
117	1.36	8	168	1356	1	92	1	336.16	34	23.22	19.47	342.44	6
92	0.90	3	226	1102	1	140	2	322.24	37.14	25.95	20.98	307.79	7
143	1.04	7	173	1236	3	0	0	230.20	28.72	18.62	15.88	294.04	8
258	1.09	6	494	984	4	0	0	188.23	29.3	19.13	15.90	293.55	9
171	1.32	4	455	896	3	0	0	209.88	34.24	23.42	20.12	278.88	10
281	0.70	2	236	1040	2	0	0	179.41	27.14	17.25	14.99	258.33	11
301	0.92	4	456	804	2	0	0	183.86	33.6	22.87	20.03	257.14	12
207	0.72	6	311	746	5	232	3	229.26	34.26	23.44	21.09	246.95	13
282	0.50	5	255	960	2	0	0	156.76	26.08	16.33	18.80	243.50	14
18	0.61	4	406	700	2	0	0	190.14	38.54	27.16	22.84	234.22	15
238	0.50	3	399	786	3	0	0	140.38	27.84	17.86	18.78	233.67	16
163	1.10	3	229	810	2	72	1	212.28	34.98	24.07	23.17	233.15	17
227	0.81	4	283	804	2	38	2	189.18	33.14	22.47	19.47	232.82	18
155	1.02	2	272	768	3	0	0	215.42	39.56	28.05	22.22	230.62	19
56	0.54	2	168	876	1	0	0	210.53	34.94	24.03	21.55	228.97	20
MP	0.60	7	176	450	2	75	2	108.89	31.15	20.74	19.00	141.51	76
FP	0.60	3	210	350	1.5	35	2	97.52	36.42	25.33	19.50	126.26	106

CS: comprehensive score; R: Ranking, MP: Male parent; FP: Female parent

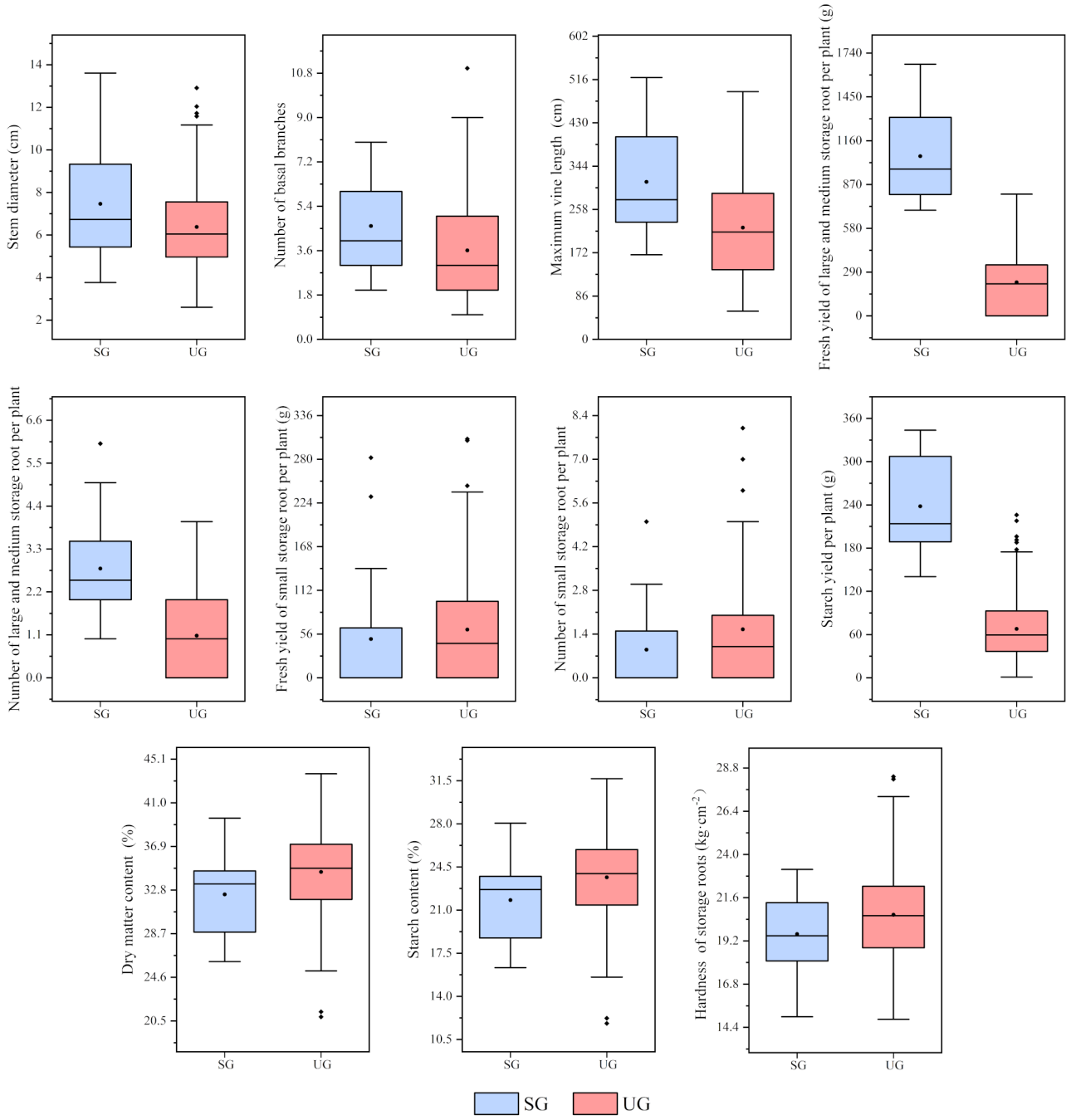

Fig. 2 Boxplot analysis of phenotypic traits of the top 20 and the rest in the F_1 population
SG, a group composed of 20 plants selected from the F_1 population; UG, a group composed of unselected plants from the F_1 population

(stem diameter, number of basal branches, maximum vine length) (correlation coefficient $r = 0.3142$, 0.3002, 0.3238, 0.2107, 0.2648, and 0.3538, respectively). Starch yield per plant exhibited highly significant positive correlations with main aboveground morphologic traits (stem diameter, number of basal branches, maximum vine length), fresh yield and the number of large and medium storage roots per plant ($r = 0.2978$, 0.2866, 0.2963, 0.9353, and 0.7174, respectively), and it showed no significant correlation with fresh yield and number of small storage roots per plant, or starch content. Dry matter content and starch content showed significant negative correlations with the number of basal branches (r=-0.1299 and −0.1303, respectively), and maximum vine length (r=-0.1674 and −0.1676, respectively), but they show no correlation with stem diameter. Hardness exhibited an

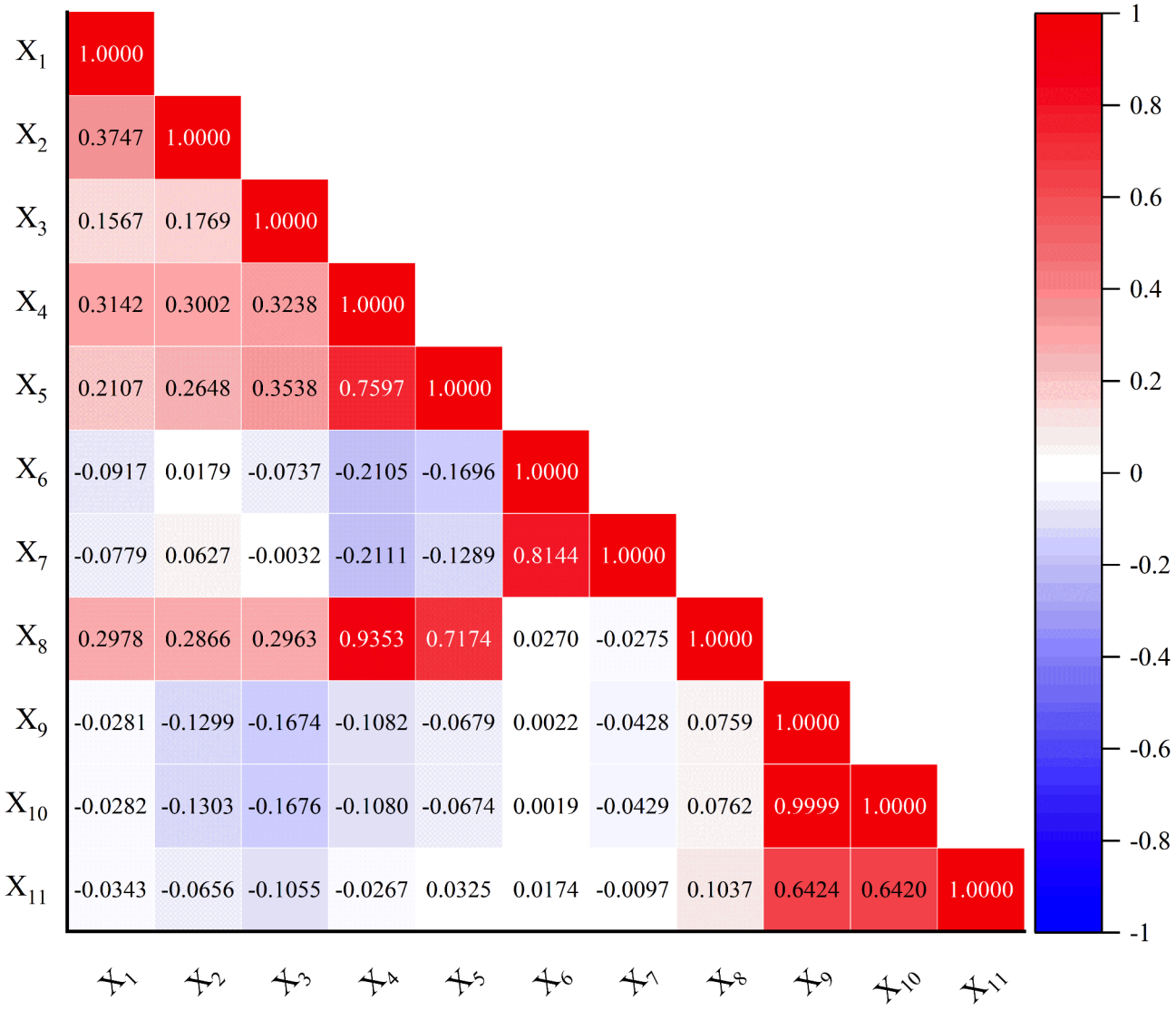

Fig. 3 The correlation analysis of 11 phenotypic traits
The correlation coefficient threshold values were α = 0.01, *r* = 0.1478 and α = 0.05, *r* = 0.1127

extremely significant positive correlation with dry matter content and starch content ($r = 0.6424$ and 0.6420, respectively), and showed no significant correlation with main aboveground morphologic traits (stem diameter, number of basal branches, maximum vine length).

Genetic diversity analysis based on SSR markers

Using 18 selected primer pairs (Table S.1), a total of 127 distinct polymorphic bands were produced by amplifying two parents and 303 hybrid F_1 populations. On average, each pair of primers can generate 7 polymorphic bands. Thirteen polymorphic bands were generated using Primer No.12, showing the highest polymorphism, while only 4 polymorphic bands were generated using primers No.11 and No.13, respectively, showing the lowest number of polymorphic bands.

The genetic similarity coefficients of the parents and 303 hybrid F_1 populations were calculated. The genetic similarity coefficients of the tested 305 materials ranged from 0.5362 to 0.9921, with an average genetic similarity coefficient of 0.7300. Among the hybrid F_1 population, the genetic similarity coefficient between No.89 and No.90 was 0.9921, which was the highest, and the genetic similarity coefficient between No.20 and No.303 was 0.5632, which was the lowest. The genetic similarity coefficient was 0.7066 between the two parents. The mean genetic similarity coefficient between the female parent and the 303 hybrid F_1 population was 0.7723, with the highest being 0.8757 with material No.184. The lowest being 0.6227 with material No.16. The mean genetic similarity coefficient between the male parent and 303 hybrid F1 population was 0.7447, with the highest being

0.8442 with material No.11. The lowest being 0.6309 with material No.205. The data showed that there were certain genetic differences between the parents, between the parents and the hybrid F_1 population, and within the hybrid F_1 population.

Comparison of detection results based on phenotypic traits and SSR markers

Analysis of genetic distance

To reveal the genetic variations among two parents and 303 hybrid F_1 populations, the genetic distances based on phenotypic detection and SSR markers were calculated (Table 5). The resulting genetic distance matrix was then used to analyze the correlation between the two methods.

The variation range of genetic distance among 305 materials (0.0001–2.4675), female parent and 303 hybrid F_1 population (0.0003–1.2377), and male parent and 303 hybrid F_1 population (0.0020–1.2013) based on phenotypic detection were mostly larger than that based on SSR markers (0.0079-0.5000, 0.1243–0.3723, and 0.1558–0.3723, respectively), indicating that the tested materials might show greater variations in phenotypic traits than that at genetic level. According to the average genetic distance among the 305 materials, the detection results based on phenotypic traits and SSR markers didn't show significant difference. However, the average genetic distance between the female parent and the 303 hybrid F_1 population (0.2238 and 0.2279 based on phenotypic traits and SSR markers, respectively) is smaller than that between the male parent and the 303 hybrid F_1 population (0.3024 and 0.2554 based on phenotypic traits and SSR markers, respectively). To determine whether there were significant differences in the genetic distances between the male parent and the F_1 population as well as between the female parent and the F_1 population, a *t*-test was conducted. The results showed that the female parent had significant smaller genetic distances with the F_1 population than that of male parent, either based on phenotypic traits ($p < 2.16 \times 10^{-3}$) or SSR markers ($p < 7.93 \times 10^{-14}$), suggesting that both phenotypic traits and genetic variation exhibit that the hybrid F_1 population may have matroclinous inheritance. The genetic distance between the parents is smaller based on phenotypic traits (0.0159) but larger based on SSR molecular markers (0.2934). Nevertheless, the hybrid F_1 population presented a high level of variations in both ways, indicating that the hybrids of sweet potato have abundant genetic diversity.

The correlation between the genetic distance matrices obtained from phenotypic detection and SSR molecular markers was calculated using the Mantel test, resulting in a correlation coefficient of $r = 0.06025$, indicating a very weak correlation. From the genetic distance matrix comparison plot with the genetic distance of SSR markers as axis X and the genetic distance of phenotypic detection as axis Y, the data distribution along the X-axis exhibits a triangular or near-normal distribution pattern, whereas the Y-axis displays a right-skewed distribution (Fig. 4).

Cluster analysis

The cluster analysis results based on phenotypic detection and SSR markers were presented in Fig. 5. Additionally, the frequency distribution analysis figure (Fig. 6) was generated for 11 phenotypic traits based on the clustering classification from the phenotypic detection, visually highlighting the primary phenotypic characteristics of each cluster.

At D = 0.10, the 305 materials can be divided into 4 categories based on phenotypic detection, with the primary characteristics of each group inferred from the phenotypic trait frequency distribution figure: Category I was comprised of 3 materials, characterized by general dry matter content and starch content, along with a higher number of basal branches and small storage roots per plant. Category II was comprised of 72 materials, characterized by relatively lower starch yield per plant. Category III was comprised of 7 materials, characterized by relatively high dry matter content, starch content, and hardness, with general starch yield per plant, relatively high fresh yield, and number of small storage roots per plant. Category IV was comprised of 223 materials (parents included), characterized by longer maximum vine length, high fresh yield and number of large and medium storage roots, low fresh yield and number of small storage roots per plant, and high starch content. At D = 0.025, Category II could be divided into 3 subcategories. Similarly, Category IV could be further divided into 6

Table 5 Genetic distance comparison between phenotypic detection and SSR markers

GD	Phenotypic detection				SSR markers			
	BM 305	BFPH	BMPH	BP	BM 305	BFPH	BMPH	BP
AGD	0.3178	0.2238	0.3024	0.0159	0.2700	0.2279	0.2554	0.2934
Max GD	2.4675 (99 and 143)	1.2377 (99 and 304)	1.2013 (99 and 305)		0.5000 (20 and 83)	0.3723 (162 and 304)	0.3723 (59 and 305)	
Min GD	0.0001 (68 and 111)	0.0003 (23 and 304)	0.0020 (202 and 305)		0.0079 (89 and 90)	0.1243 (184 and 304)	0.1558 (110 and 305)	

GD: Genetic distance, AGD: Average genetic distance, Max GD: Maximum genetic distance, Min GD: Minimum genetic distance, BM 305: Between 305 materials, BFPH: Between female parent and hybrid F_1 population, BMPH: Between male parent and hybrid F_1 population, BP: Between male and female parents

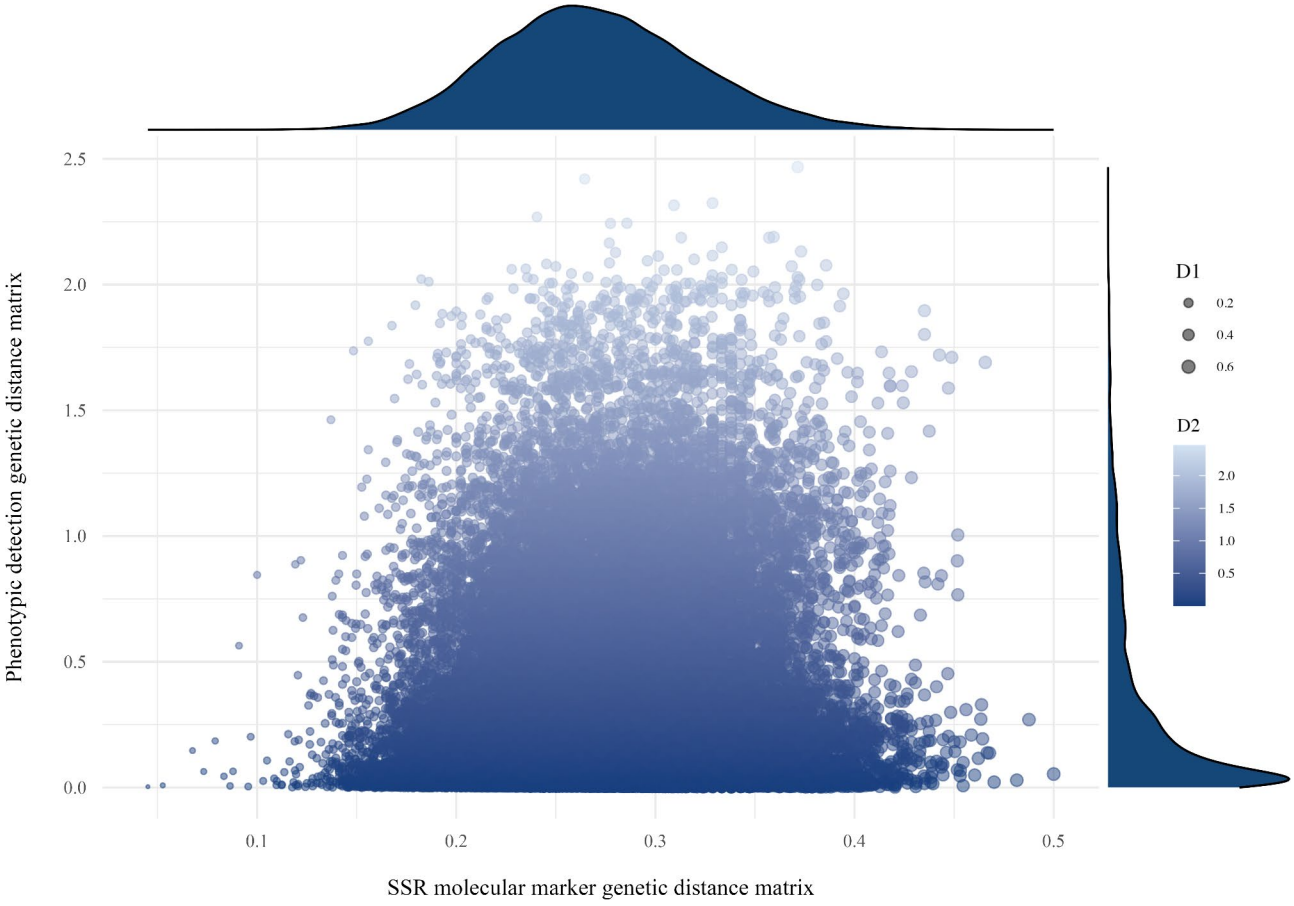

Fig. 4 Genetic distance matrix comparison of SSR markers and phenotypic detection
D1, Genetic distance based on SSR maker; D2, Genetic distance based on phenotypic detection

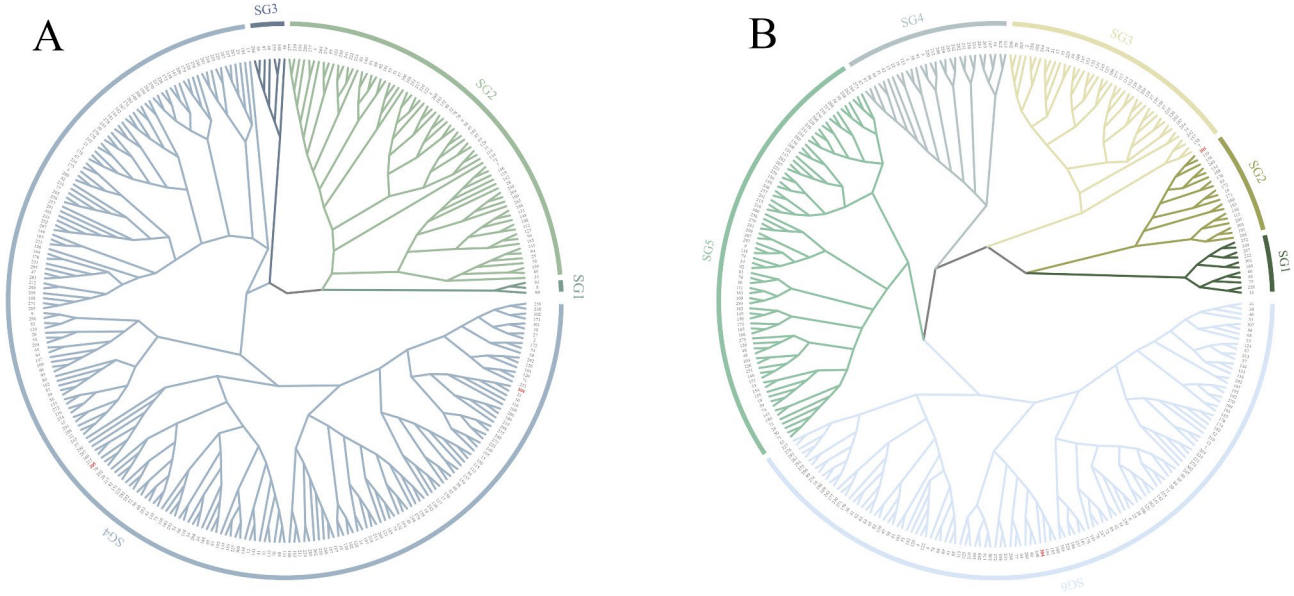

Fig. 5 Cluster analysis based on phenotypic detection (**A**) and SSR markers (**B**)
The different colors represent Category I-IV (SG1-SG4) identified by cluster analysis based on phenotypic detection in Fig. 2A, and the different colors represent Category I-VI (SG1-SG6) identified by cluster analysis based on SSR markers in Fig. 2B. The female parent (304) and the male parent (305) are highlighted in red in the figure. The same applies to Fig. 7

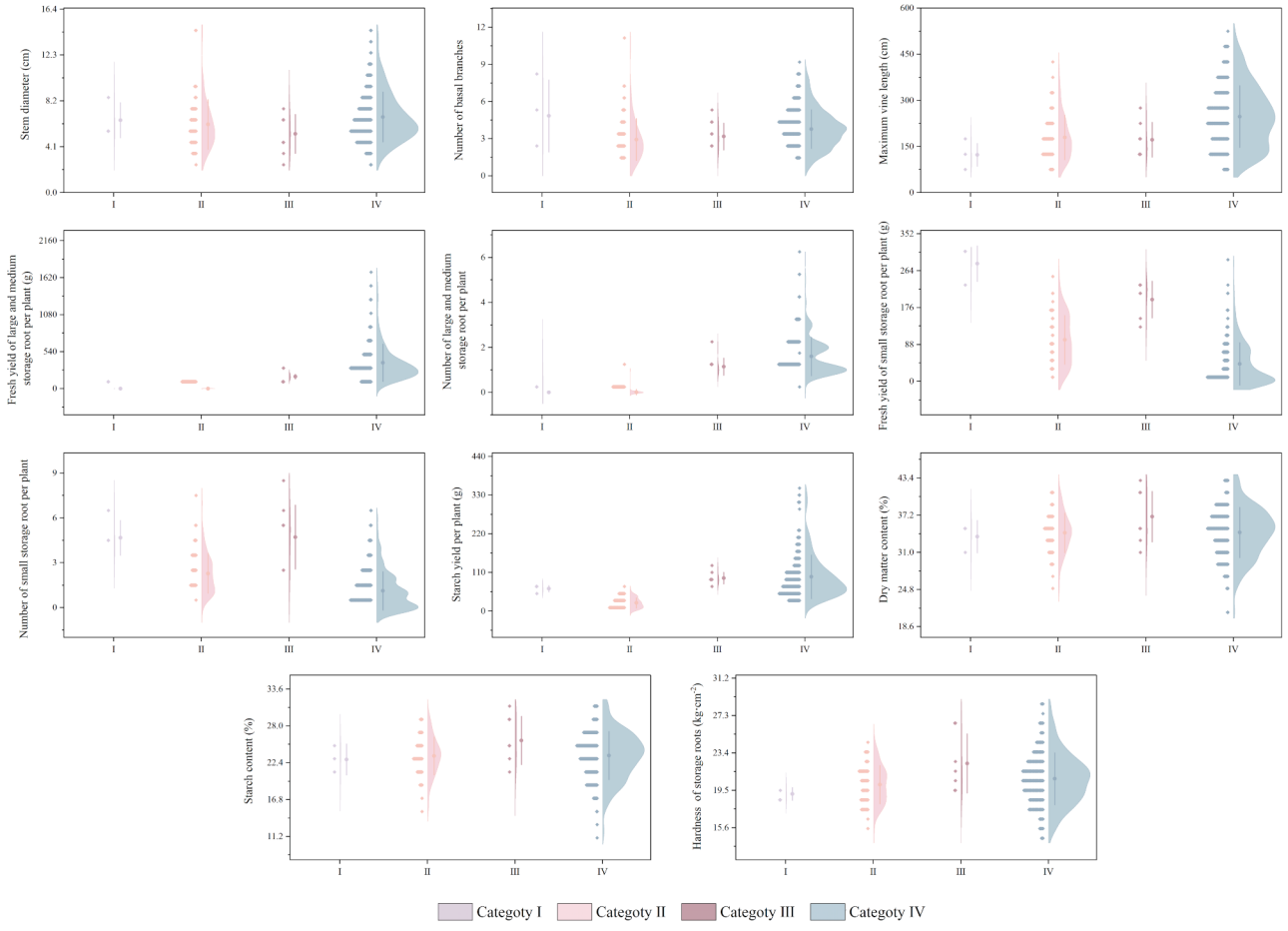

Fig. 6 Frequency distribution of 11 phenotypic traits in various clusters based on phenotype detection clustering analysis results

subcategories, with the female and male parents in different subcategories.

The cluster analysis based on SSR markers showed that when the 305 materials were divided into two categories, the female and male parents belonged to different categories. Category I was comprised of 30 materials (including the male parent). In comparison, Category II was comprised of 275 materials (including the female parent), which indicated the relatively far genetic distance between the two parents and the matroclinous inheritance in the hybrid F_1 population. Moreover, Category I can be divided into 2 subcategories, and Category II can be divided into 4 subcategories. In this way, there were a total of 6 categories: Category I contained 11 materials, Category II contained 19 materials (including the male parent), Category III contained 43 materials, Category IV contained 30 materials, Category V contained 78 materials, Category VI contained 124 materials (including the female parent, and could be further divided into 2 subcategories).

Cluster analysis based on both phenotypic detection and SSR markers showed that the hybrid F_1 population has rich genetic diversity. However, the genetic distance between the two parents was relatively far based on SSR markers and was relatively close according to the phenotypic detection. A comparative analysis was conducted by aligning the clustering results from both methods (Fig. 7). While differences between the two sets of results are evident, a degree of consistency was also observed, reflecting the genetic diversity of the hybrid F_1 population from different perspectives.

Discussion

Phenotypic segregation and trait variation in hybrid F_1 population of sweet potato

In the study, a hybridization was conducted between the high starch content sweet potato variety Yushu No.12 and the high yield sweet potato variety Luoxushu No.9, resulting in broad trait segregation within the hybrid F_1 population. In the frequency distribution of phenotypic traits within the F_1 population, only quality traits (dry matter content, starch content, and hardness) and maximum vine length exhibited normal distribution. In contrast, yield traits (fresh yield and, number of storage roots, and starch yield per plant) did not follow a normal distribution and showed high kurtosis and skewness. It

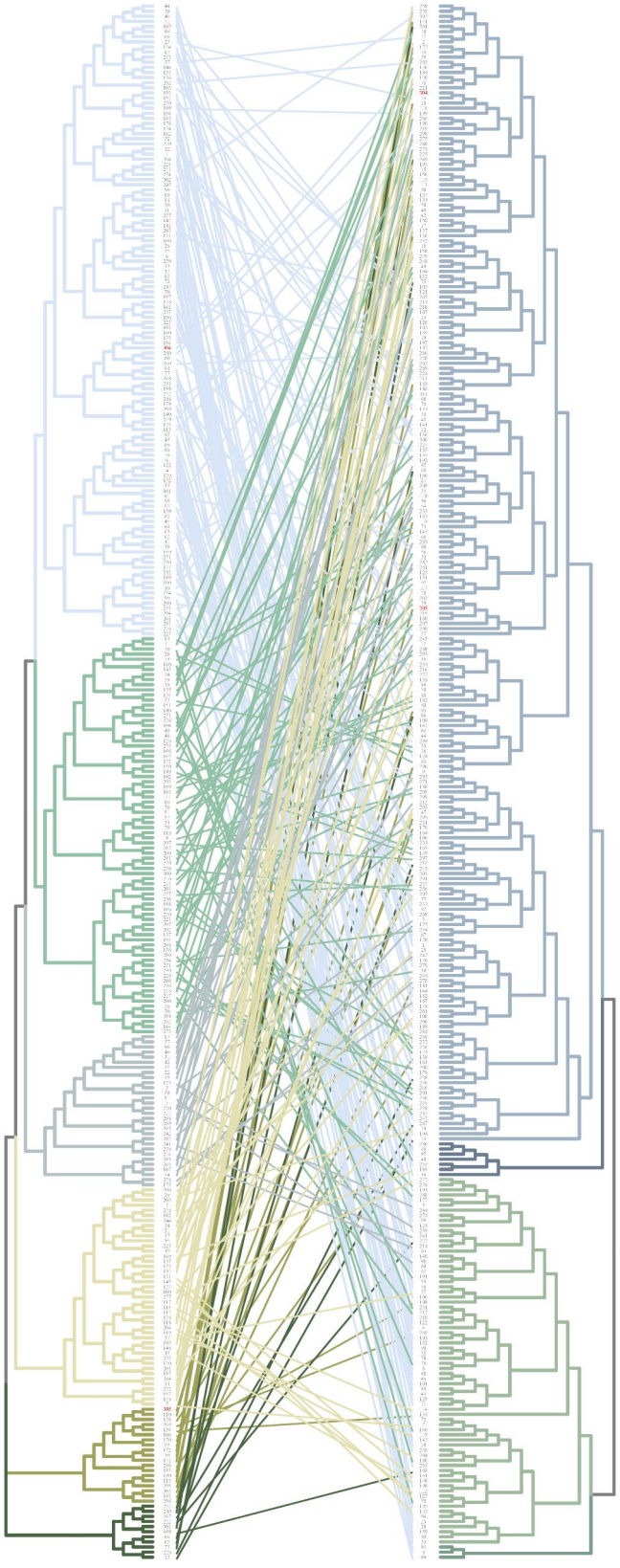

Fig. 7 Comparison of cluster analysis based on phenotypic detection and SSR markers
The dendrogram on the left represents the results of the cluster analysis based on SSR molecular markers, while the dendrogram on the right is based on phenotypic detection. Identical plant numbers are connected by lines in the middle. For clarity, the color of the connecting lines follows the dendrogram based on SSR makers

was reported that quality traits are less influenced by the environment [24], but mainly controlled by genetic factors [34]. Much evidence shows that traits controlled by multiple genes exhibit continuous variation in the F_1 generation, conforming to a normal distribution or a skewed normal distribution [35, 36, 37]. However, as yield traits are more significantly affected by environmental factors [24], thus environmental influences can lead to extremely skewed distributions [38].

According to statistical analysis of phenotypic detection, yield traits exhibited the greatest variation, followed by morphological traits (stem diameter, maximum vine length, and number of basal branches), with quality traits showing the least variation. These results may be attributed to the fact that these yield and quality traits in sweet potato are complex and predominantly quantitative traits controlled by multiple genes, which are significantly influenced by genetic effects, leading to complex genetic patterns [39, 40]. The underlying mechanisms contributing to the genetic variation of these traits still require an in-depth investigation on the genes associated with the relevant traits. Furthermore, to identify the genes controlling starch properties and yield trait are also critical to breed high-starch and high-yield sweet potato varieties through molecular breeding.

Matroclinous inheritance characteristics in hybrid F_1 population of sweet potato

Based on the statistical analysis of phenotypic traits in the hybrid F_1 population, it could be suggested that morphological traits, yield traits, and quality traits might exhibit matroclinous inheritance. The genetic distances calculated from phenotypic detections and SSR markers indicated that the F_1 population was genetically closer to the female parent than to the male parent. Furthermore, the cluster analysis results derived from SSR markers provided additional robust evidence supporting the matroclinous inheritance pattern. This may be due to the influence of sweet potato's plastogene, which generally followed matrilineal inheritance [41]. This is similar to the results of previous studies [25]. However, this finding still requires further verification through reciprocal crossing experiments across multiple hybrid combinations, and the underlying genetic mechanism in sweet potato also need to be thoroughly investigated. Consequently, when selecting parents for sweet potato hybrid breeding, it is advisable to prioritize the female parent.

The advantages and disadvantages of the comprehensive score model

In the comprehensive score model established in this study, offspring with higher scores are selected to receive variety tests, and this provides a simple and convenient method for breeding improved new varieties and shortening the breeding period. However, it should be noted that the top 20 plants selected using the scoring model exhibited significantly better yield and morphological traits compared to quality traits. Therefore, this comprehensive scoring model is more suited for selecting high-yield materials. When selecting other traits, it is necessary to consider as many character indexes as possible to improve the scoring system's comprehensiveness and reliability, ensuring its broad applicability and accuracy. Moreover, this selection model enables more efficient identification of improved varieties, and will help to provide valuable genetic material and an experimental foundation for further investigation on the genes and molecular mechanisms regulating these key traits.

Selecting high-starch sweet potato based on hardness

Previous studies aimed at aboveground traits, and underground traits, and the correlation between the two showed varying results [42, 43, 44, 45, 46]. The correlation analysis of different traits in the hybrid F_1 population of sweet potatoes conducted in this study also differs from previous findings [31, 47, 48]. In fact, variations in research methods, germplasm populations, or growing environments, along with the multifactorial influence on traits, might result in different correlations, leading to differences in the deduced breeding methods. In this study, the hardness of storage roots was calculated by the resulting hardness values showed a highly significant positive correlation with starch content ($r = 0.6420$). This result provides a theoretical basis for the selection of high starch content sweet potato germplasms based on storage root hardness, and suggests an simple and rapid approach for the preliminary selection of high starch content progeny. In the breeding practice, the starch content could be preliminarily estimated by the hardness test in the field, followed by detailed starch content determination on breeding materials with ideal hardness, which can effectively reduce the number of tested breeding materials, and thereby improve breeding efficiency and reduce the cost of trait measurement.

The abundant genetic diversity and superior evaluation method in the hybrid F_1 population of sweet potato

Sweet potato was primarily vegetatively propagated, but it can also reproduce sexually under suitable natural or controlled conditions [49, 50]. The hybrid F_1 population in this study exhibited extensive variation, with high genetic diversity indices based on phenotypic traits, indicating substantial genetic diversity. Genetic distance and cluster analysis based on phenotypic detection and SSR molecular markers further corroborated the profound genetic diversity within the hybrid F_1 population. This may be attributed to the inherently complex genetic backgrounds of the sweet potato parents, which are

typically heterozygous with traits controlled by multiple genes [26, 27]. However, the Mantel test revealed that the correlation between the genetic distance matrix obtained from SSR molecular markers and phenotypic detections was not significant ($r = 0.06025$). Moreover, there were substantial differences in the genetic distances between the parents as determined by the two methods, indicating differences in the analysis of sweet potato genetic diversity. Since phenotypic traits are shaped by natural and artificial selection, while molecular markers remain unaffected by these factors, the two methods respectively reflect the rich genetic diversity of the hybrid F_1 population at the molecular and phenotypic levels, further confirming that sweet potato phenotypic traits are the result of genotype-environment interactions [51]. Additionally, the comparison plot of the genetic distance matrix from SSR molecular markers and phenotypic detections showed a triangular or normal distribution along the X-axis (SSR molecular marker genetic distance matrix), indicating greater genetic stability, which is more predictable in breeding. In contrast, the Y-axis (phenotypic detection genetic distance matrix) exhibited a skewed distribution, suggesting that certain phenotypic traits may show bias under specific genotypic or environmental conditions. This pattern suggests that SSR molecular markers provide a more precise and reliable evaluation of genetic diversity in sweet potato hybrid F_1 populations compared to phenotypic detections [52].

The results obtained in this study not only facilitates the elucidation of the genetic networks controlling important morphological, yield and quality traits in sweet potato, but also advances molecular breeding efforts, offering a crucial breakthrough for overcoming breeding challenges.

Conclusions

The comprehensive scoring model and the preliminary selection method based on the hardness of storage root provide a simple and effective tool for developing high-yield and high-starch sweet potato materials. Both phenotypic detections and SSR molecular markers indicate that the hybrid F_1 population might exhibit matroclinous inheritance, suggesting that the female parent should be prioritized in hybrid breeding parent selection. The sweet potato hybrid F_1 population showed rich genetic diversity, and compared to phenotypic detections, SSR molecular markers offer a more precise and reliable method for studying genetic diversity.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12870-025-06166-w.

Supplementary Material 1

Supplementary Material 2

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Author contributions
JWW: Writing– review & editing, Formal analysis, Visualization, Software. YXL: Writing– review & editing, Formal analysis, Visualization, Software. WRZ: Resources, Data curation, Investigation. XYR: Methodology, Conceptualization. GML: Data curation, Validation. RJC: Investigation, Data curation. ZHZ: Resources, Methodology, Validation, Conceptualization. DBT: Resources, Methodology, Conceptualization. HXL: Writing– original draft, Methodology, Investigation, Data curation, Visualization. JCW: Supervision, Project administration, Conceptualization. KZ: Writing– review & editing, Methodology, Supervision, Project administration, Funding acquisition, Conceptualization. All authors reviewed the manuscript.

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Data availability
The datasets generated and/or analyzed during the current study are available in the figshare repository. The original phenotypic data is available at https://doi.org/10.6084/m9.figshare.27860523.v2, and the SSR 0-1 matrix data is available at https://doi.org/10.6084/m9.figshare.27860541.v1.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Clinical trial number
Not applicable.

Competing interests
The authors declare no competing interests.

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