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RESEARCH ARTICLE

Genetic potential unravelling for anaerobic germination tolerances in North-eastern Indian rice (*Oryza sativa* L.) germplasm

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Abstract

Anaerobic germination is one of the constraints faced by direct-seeded rice (DSR) plants, causing poor and irregular germination. In this study, 281 rice germplasm lines were screened for anaerobic germination. Based on the phenotypic variation of root length, coleoptile length and percentage of germination, 24 genotypes were identified as anaerobic germination tolerant. The correlation analysis showed a significant association among phenotypic traits in aerobic and anaerobic germination. Out of 281, 24 rice germplasm lines were found to be tolerant to anaerobic germination based on a positive response index of >0.1. The genetic diversity among the 48 selected germplasm using 48 SSR markers of 12 rice chromosomes revealed a prevalence of enough diversity for marker-trait association analysis. The PIC value ranged from 0 to 0.375, with the maximum (0.375) in RM16238, RM7311, RM20228, RM22321, RM25866 and RM26603 markers. The dendrogram based on UPGMA-based clustered analysis and population structure clustered the 48 individuals into two major groups. Marker-traits association analyses identified five SSR markers (RM20948, RM26033, RM16730, RM23732 and RM25866) that were strongly associated with root length and coleoptile length with a phenotypic variance of 1.1 to 9.9%. These findings provide valuable insights into the genetic architecture and population structure underlying anaerobic germination tolerance in rice, facilitating future breeding efforts to develop improved DSR varieties.

Keywords- Anaerobic germination, rice, genetic diversity, direct seeded rice, DNA markers

Introduction

Rice (*Oryza sativa* L.) is a staple food for more than half of the world's population; nevertheless, the rice agri-food sector as a whole is fast evolving, particularly in developing countries. Irrigated rice ecosystems cover 55% of the world's rice-growing area and produce 75% of worldwide rice production (Mahender et al. 2015; Su et al. 2021). However, due to the increasing shortage of these resources, the water, energy, and labor-intensive system of transplanted puddled rice is gradually replaced by direct-seeded rice (Nagargade et al. 2018). The biggest barrier to the large-scale adoption of DSR in water is abiotic stress anaerobic germination (AG). Anaerobic germination is the ability of the rice seeds to germinate and grow in the absence of oxygen. Anaerobic germination contributes to rapid seedling establishment, enabling plants to cope with submersion and enrich crop performance. Breeding initiatives need to consider the genetic components that confer tolerance, particularly since climate change could make flooding events more frequent. Recently, several investigations for anaerobic germination in rice have been conducted and genomic regions or QTLs related to anaerobic germination have been mapped and

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identified through biparental mapping, genome-wide association mapping, etc. (Yang et al. 2022; Hsu and Tung 2015; Zhang et al. 2017). The trehalose-6-phosphate (T6P) phosphatase gene (*OsTPP7*), which is important in T6P metabolism under anaerobic stress, *OsTPP7* promoted T6P turnover, boosting starch mobilization and driving the development kinetics of the germinating embryo and the elongation of the coleoptile, which improved AG tolerance (Kretzschmar et al. 2015).

There are untapped genetic resources and traditional rice genotypes in the north eastern state of India for the response to anaerobic germination (Devi et al. 2024; Ngangkham et al. 2020). To identify donors for direct seeded rice with anaerobic germination tolerance, a set of 281 rice germplasm from North Eastern states of India were screened using standard protocols. For screening of anaerobic germination tolerance, healthy rice seeds were treated with Bavistin fungicide (1%) for 30 minutes followed by washing with distilled water three times. The seeds were further surface sterilized with a 1% sodium hypochlorite solution for 5 minutes and washed with distilled water thrice. Around 30 seeds for each genotype were taken for treatment. The seeds were given treatment for anaerobic germination in a plastic bottle with a 5 cm height of water above the seeds and kept under dark conditions at 28 to 30°C temperature inside the germinator (Caltan NSW-191 Seed Germinator). For control, the same number of seeds for each genotype were incubated in the same size plastic bottle with moisture and kept under dark conditions at 28 to 30°C temperature inside the same germinator for 10 days. The observation data, such as coleoptile length, root length, and germination percentage of 281 rice lines, including IR-36 as a susceptible genotype, were recorded after 10 days of treatment. Based on the recorded data, tolerant rice lines were selected based on the positive response index (R_i).

$$\text{Response index } (R_i) = \text{Coleoptile length } (CL_t)(\text{treatment}) - \text{Coleoptile length } (CL_c) \text{ (control)}$$

Mean performance and correlation studies

The average coleoptile length, root length, and germination percentage were found to be 2.016 ± 1.862, 2.061 ± 1.249 cm, and 74.718 ± 26.658%, respectively, in the control or aerobic condition (Table 1). The maximum coleoptile length and root length were found in IRGC 127652 and IRGC 127714 with 11.1 ± 0.012 and 6.78 ± 0.245 cm, respectively, in the aerobic condition. However, the average coleoptile length, root length, and germination percentage in anaerobic conditions were found to be 0.689 ± 0.865, 0.371 ± 0.101 cm, and 54.7330 ± 32.574%, respectively.

The correlation coefficients among phenotypic traits control are shown in Table 2. In aerobic conditions, the coleoptile length was significantly correlated with root length (r = 0.319, p = 0.01). Meanwhile, germination percentage was also significantly correlated with coleoptile length (r = 0.297, *p* = 0.01) and root length (r = 0.223, *p* = 0.01). In anaerobic condition, the coleoptile length was negatively correlated with root length (r = -0.675, *p* = 0.01), whereas germination percentages were significantly and positively correlated with coleoptile length (r = 0.158, *p* = 0.05) as well as with root length (r = 0.227, *p* = 0.01).

Identification of anaerobic germination tolerance based on Response Index (Ri) values

The maximum and minimum response index (R_i) values among the 281 rice germplasm were found to be 2.0 (Phoutum Mah) and -9.66 (IRGC 26390), respectively, with an average of -1.32 ± 1.563. Out of these 281 rice genotypes, 24 rice germplasm were found to have with positive response index of >0.1 (Table 3). The 24 rice genotypes are Sopa Kemenga, Phoutum Mah, Lesem Jang, Chakhao Bishnupur, Ereima, CCpur 100, Phungcham Mah, Changphoi Awangba, Naga Special, Ching Chakhao, Tarasang, SARS-2, Mutsuku, Mukhok Mujeh, Wonder Rice, Haorei Machang, Jenil Kajie Phek, Phat Sen, Teyang Retjang, Khemaru, Phoural Utlou, Mara, Kakcheng Phou and Phouren Phou.

A total of 48 SSR markers, four each from 12 rice chromosomes with uniform distribution, were collected from the Gramene database and used to study the genetic diversity of selected 48 rice germplasm based on their response index (R_i), including highest, medium and lowest values from 281 rice germplasm (Supplementary Table S1). The PIC value ranged from 0 to 0.375. The maximum (0.375) PIC value was recorded in RM20228, RM21330, RM26033, and RM26603. The observed heterozygosity (H_{Obs}) ranged

Table 1. Statistical analysis of phenotypic data of 281 rice germplasm lines under aerobic and anaerobic conditions

	Traits	Mean ± SD	Maximum	Minimum	Range
Control or aerobic condition	Root length (cm)	2.063 ± 1.302	13.3	0	13.3
	coleoptile length (cm)	2.483 ± 2.014	11.1	0	11.1
	Germination %	89.558 ± 14.512	100	0	100
Anaerobic condition	Root length (cm)	0.369 ± 0.103	0.6	0	0.6
	coleoptile length (cm)	1.023 ± 1.332	10	0	10
	Germination%	67.046 ± 28.962	100	0	100

Table 2. Pearson correlation of the coleoptile length, root length, and germination percentage of 281 rice germplasm

Conditions	Traits	Coleoptile length	Root length
Control or aerobic condition	Root length	0.319**	1
	Germination percent%	0.297**	0.223**
Anaerobic condition	Root length	-0.675**	1
	Germination percent%	0.158*	0.227**

*,** denotes significance of P value < 0.1 &< 0.001, respectively

Table 3. Response Index (Ri) values of selected 24 rice germplasm with anaerobic germination tolerance

S No.	Germplasm	Shoot length under control (cm)	Shoot length under treatment (cm)	Response index (Ri)
1.	Sopa Kemenga	2.6 ± 0.12	3.3 ± 0.67	0.7
2.	Phoutum Mah	2.30 ± 0.89	4.3 ± 0.34	2.0
3.	Lesem Jang	2.3 ± 0.12	2.6 ± 0.89	0.3
4.	Chakhao Bishnupur	2.0 ± 0.86	2.7 ± 0.75	0.7
5.	Ereima	1.9 ± 1.18	2.0 ± 0.56	0.1
6.	CCpur 100	1.8 ± 0.23	2.5 ± 0.45	0.7
7.	Phungcham Mah	1.6 ± 0.54	1.8 ± 0.65	0.2
8.	Changphoi Awangba	1.5 ± 0.12	2.4 ± 0.24	0.9
9.	Naga Special	1.1 ± 0.26	1.9 ± 0.11	0.8
10.	Ching Chakhao	0.9 ± 0.18	2.0 ± 0.34	1.1
11.	Tarasang	0.9 ± 0.25	1.2 ± 0.56	0.3
12.	SARS-2	0.7 ± 0.78	1.3 ± 0.78	0.6
13.	Mutsuku	0.6 ± 0.36	0.7 ± 0.56	0.1
14.	Mukhok Mujeh	0.6 ± 0.59	0.9 ± 0.35	0.3
15.	Wonder Rice	0.5 ± 0.48	1.2 ± 0.64	0.7
16.	Haorei Machang	0.8 ± 0.57	0.9 ± 0.78	0.1
17.	Jenil Kajie Phek	0.5 ± 0.26	0.6 ± 0.64	0.1
18.	Phat Sen	0.4 ± 0.63	1.4 ± 0.84	1
19.	Teyang Retjang	0.1 ± 0.45	0.3 ± 0.66	0.2
20.	Khemaru	0.7 ± 0.94	0.8 ± 0.57	0.1
21.	Phoural Utlou	0.9 ± 0.12	1.0 ± 0.77	0.1
22.	Mara	0.8 ± 0.78	0.9 ± 0.15	0.1
23.	Kakcheng Phou	0.9 ± 0.45	1.1 ± 0.23	0.2
24.	Phouren Phou	0.5 ± 0.67	0.7 ± 0.18	0.2

from 0 to 0.846. The expected heterozygosity (H_{Exp}) ranged from 0 to 0.506. To assess the genetic relationships among the selected 48 rice germplasm, a UPGMA method was categorized into three main groups named I, II and III (Fig. 1).

Genetic association

For marker-trait association analysis, genotypic data of 48 SSR markers and corresponding phenotypic data of coleoptile length, root length, and germination percentage were used for association analysis using the GLM algorithm in TASSEL 5.2.27 version software (Bradbury et al. 2007). The genetic association analysis of root length under anaerobic germination conditions (AG) showed significant associations with the markers RM20948, RM16730, and RM26033 at chromosome number 7,11, and 4 with R^2 values of 0.136, 0.145, and 0.099, respectively (Table 4). This suggests that genetic variations at these markers contribute significantly to the observed variations in root length under anaerobic germination conditions. Similarly, shoot length under anaerobic germination conditions (AG) showed significant associations with the markers RM23732 and RM25866 at chromosome numbers 9 and 10 with R^2 values of 0.112 and 0.123, respectively. The root length and coleoptile length under aerobic conditions also show significant associations with certain markers such as RM24071, RM25262, RM20948, and RM27815 at chromosome numbers at 9, 10, 7 and 12 show significant associations with R^2 values of0.111, 0.173, 0.117 and 0.129, respectively indicating genetic influences on these traits even under aerobic conditions. For the response index (RI), the markers RM6738 and RM26033 at chromosome numbers 1 and 11 show significant associations with R^2 values of 0.094 and 0.124, respectively. These results suggest specific genetic markers that may be involved in regulating root and coleoptile length under

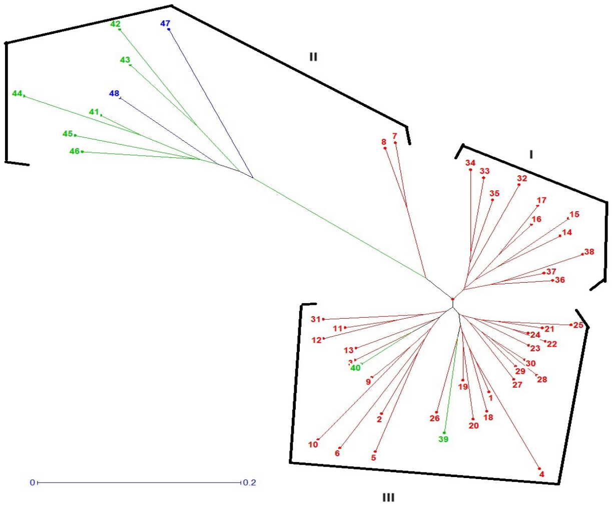

Fig. 1. Clustered analysis of 48 rice genotypes using 48 SSR markers. Landraces is denoted by red color, cultivars (green) and black rice (blue) are divided into three groups I, II and III and again subdivided into subgroups IA, IB, IIA, IIB, IIIA, and IIIB

Table 4. Genetic association of SSR marker under anaerobic germination (AG) and control/aerobic germination conditions

S. No.	Traits	Markers	Chromosome	Marker- R^2
1.	Root length (AG)	RM20948	7	0.1361999**
2.		RM26033	11	0.0991227*
3.		RM16730	4	0.1452991**
4.	Shoot length (AG)	RM23732	9	0.1119931*
5.		RM25866	10	0.1233559*
6.	Root length (control)	RM24071	9	0.111747545*
7.		RM25262	10	0.1736611339**
8.	Shoot length (control)	RM20948	7	0.117587985*
9.		RM27815	12	0.129125899*
10.	Response Index (Ri)	RM6738	1	0.093965054*
11		RM26033	11	0.124228318*

* & ** denotes significant P value at <0.05 and <0.01, respectively.

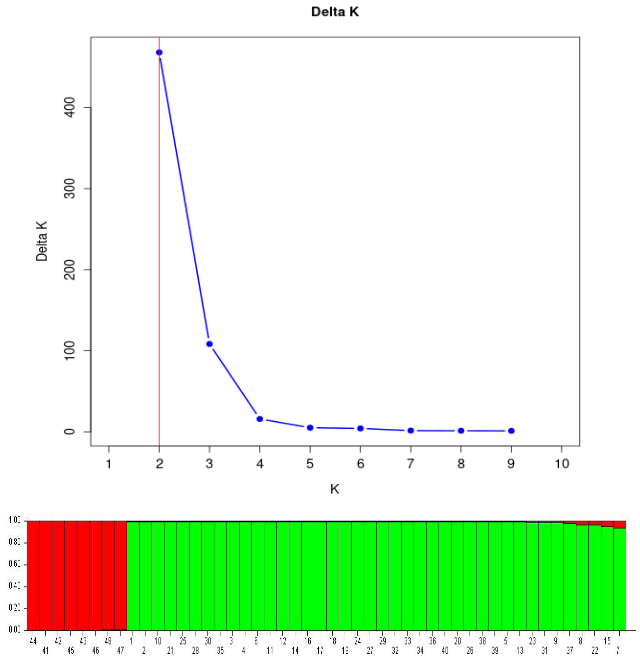

Fig. 2. (A) The maximum of ad-hoc measure Δk determined at k= 2, in which the entire population can be grouped into two subgroups and (B) Population structure of 48 genotypes arranged based on inferred ancestry. Based on the membership fractions, the accessions with a probability of >70% were assigned to corresponding subgroups. Each sample is represented by a single vertical line broken into k (k=2) colored segments, with lengths proportional to each of the K-inferred clusters. Different colour within a group indicates the proportion of shared ancestry with other groups

anaerobic germination conditions, as well as the overall response of the plant to such conditions.

The associated markers showed a phenotypic variance of 1.1 to 9.9%. The significance of these markers could provide insights into the genetic mechanisms underlying anaerobic germination tolerance, highlighting significant marker trait associations and their respective contributions to the phenotypic variance observed in root length, coleoptile length, and response index under anaerobic germination conditions.

The genetic association of root length (AG) indicates RM20948 ($R^2 = 0.1362$*), a strong and significantly associated RM26033 ($R^2 = 0.0991$), a significant but weaker associated, RM16730 ($R^2 = 0.1453$*), the strongest associated for root length under anaerobic conditions, suggesting it could be a key marker for improving this trait. For coleoptile length (AG), RM23732 ($R^2 = 0.1120$) indicates a moderate and significant association and RM25866 ($R^2 = 0.1234$*), also a significant association, suggesting both markers may be useful for selecting shoot traits in low-oxygen environments. For response index (RI), RM6738 ($R^2 = 0.0939$*), a weaker but still significant association, indicating it may have some influence on overall plant performance andRM26033 ($R^2 = 0.1242$*), suggesting a stronger role in the response index, indicating it may affect plant adaptability under aerobic environment during the germination stage.

The present study enhances our understanding of the genetic architecture and population structure associated with rice's ability to withstand anaerobic germination. The complex correlations between germination qualities in anaerobic conditions were brought to light by the correlation analysis. The basis for marker-assisted selection is established by the identification of particular markers related to desirable features. This process may accelerate the breeding of rice varieties that are directly seeded and more suitable for low-oxygen environments.

Supplementary material

Supplementary Tables S1 and S2 are provided with the text, which can be accessed at www.isgpb.org

Authors' contribution

Conceptualization of research (UN); Designing of the experiments (UN, JH, SR, PWS, KR); Contribution of experimental materials (UN, JH, HLD, AK, KR); Execution of field/lab experiments and data collection (UN, JH); Analysis of data and interpretation (KRS, AK, SPD); Preparation of the manuscript (UN, JH, CBD).

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Supplementary Table S1. Genetic diversity analysis with the parameters of estimation of k, N, H_{obs}, H_{Exp}, PIC, HW, and F in 48 SSR markers

S. No.	Markers	Chromosome number	k	N	H_{Obs}	H_{Exp}	PIC	HW	F(Null)
1.	RM495	1	2	48	0.042	0.474	0.359	***	0.8364
2.	RM6681	1	2	48	0.021	0.205	0.182	ND	0.7743
3.	RM6738	1	2	47	0.106	0.374	0.301	ND	0.5526
4.	RM12160	1	2	47	0	0.042	0.041	ND	0.5017
5.	RM12293	1	2	48	0.042	0.281	0.239	ND	0.7304
6.	RM12404	2	2	48	0	0.041	0.04	ND	0.4965
7.	RM13199	2	2	47	0.064	0.461	0.352	***	0.754
8.	RM13775	2	2	47	0	0.256	0.221	ND	0.9655
9.	RM14125	2	2	45	0	0.463	0.353	***	0.9988
10.	RM14320	3	2	48	0	0.281	0.239	ND	0.9756
11.	RM14379	3	2	48	0	0.379	0.305	ND	0.9947
12.	RM14981	3	2	46	0	0.482	0.363	***	0.9992
13.	RM15539	3	2	47	0	0.157	0.144	ND	0.8733
14.	RM16238	3	2	48	0.042	0.504	0.375	***	0.8457
15.	RM16341	4	2	47	0.702	0.461	0.352	*	-0.2128
16.	RM16730	4	2	42	0.357	0.38	0.305	ND	0.0244
17.	RM17277	4	2	48	0.063	0.266	0.229	ND	0.6109
18.	RM17599	4	2	48	0	0.041	0.04	ND	0.4965
19.	RM17803	5	2	44	0	0.238	0.208	ND	0.9556
20.	RM18239	5	2	48	0	0.252	0.218	ND	0.9633
21.	RM18625	5	2	12	0.167	0.507	0.368	ND	0.4894
22.	RM19039	5	2	46	0	0.123	0.114	ND	0.808
23.	RM19303	6	2	48	0.167	0.474	0.359	***	0.4754
24.	RM7311	6	2	48	0	0.505	0.375	***	0.9995
25.	RM20228	6	2	48	0.833	0.505	0.375	***	-0.25
26.	RM20746	6	2	48	0.063	0.205	0.182	ND	0.5183
27.	RM20948	7	2	44	0	0.301	0.253	ND	0.9818
28.	RM21330	7	2	48	0.833	0.491	0.368	***	-0.2631
29.	RM21776	7	2	47	0.021	0.139	0.128	ND	0.6542
30.	RM22073	7	2	47	0.277	0.502	0.373	NS	0.2843
31.	RM22321	8	2	47	0.021	0.504	0.375	***	0.9179
32.	RM22881	8	2	48	0	0.252	0.218	ND	0.9633
33.	RM23076	8	2	48	0.063	0.503	0.374	***	0.7769
34.	RM23528	8	2	48	0	0.252	0.218	ND	0.9633
35.	RM23732	9	2	10	0.1	0.479	0.351	ND	0.6395
36.	RM24071	9	2	46	0.13	0.318	0.265	ND	0.4137
37.	RM24309	9	2	48	0	0.281	0.239	ND	0.9756
38.	RM25093	10	2	48	0.042	0.418	0.328	ND	0.8158
39.	RM25262	10	2	47	0.021	0.502	0.373	***	0.9175
40.	RM25675	10	2	46	0	0.123	0.114	ND	0.808

41.	RM25866	10	2	46	0.13	0.505	0.375	***	0.5856
42.	RM26033	11	2	47	0.83	0.497	0.371	***	-0.2557
43.	RM26603	11	2	48	0.083	0.504	0.375	***	0.7138
44.	RM27096	11	2	48	0.354	0.468	0.356	NS	0.1335
45.	RM27363	11	2	48	0.5	0.462	0.353	NS	-0.0444
46.	RM27487	12	2	48	0.021	0.368	0.298	ND	0.8879
47.	RM27815	12	2	39	0	0.36	0.292	ND	0.9926
48.	RM28379	12	2	48	0.042	0.474	0.359	***	0.8364
Mean			2	45.42	0.12	0.35	0.27	-	0.63

Supplementary Table S2. Population structure group of genotypes based on inferred ancestry values

Sample No.	Germplasm	Inferred Ancestry		Structure group	Subtype
		Q1	Q2		
1	Chingphou	0.001	0.999	SG2	Landrace
2	GP/K/10 Mema Katwa	0.001	0.999	SG2	Landrace
3	China-1	0.002	0.998	SG2	Landrace
4	Phungcham Mah	0.002	0.998	SG2	Landrace
5	Rezose Phek	0.004	0.996	SG2	Landrace
6	CCpur	0.002	0.998	SG2	Landrace
7	Wainem	0.063	0.937	SG2	Landrace
8	Manen Jang	0.03	0.97	SG2	Landrace
9	Arunachal-1	0.014	0.986	SG2	Landrace
10	Lesem Jang	0.001	0.999	SG2	Landrace
11	Bvhman Mon	0.002	0.998	SG2	Landrace
12	Kba Jawai	0.002	0.998	SG2	Landrace
13	Pumpha Mah	0.006	0.994	SG2	Landrace
14	CCpur 100	0.002	0.998	SG2	Landrace
15	WR-1-9-1-1	0.049	0.951	SG2	Landrace
16	Phat Sen	0.002	0.998	SG2	Landrace
17	Tonakena Phek	0.002	0.998	SG2	Landrace
18	Tsuk Nyiko	0.002	0.998	SG2	Landrace
19	Kwanghai	0.002	0.998	SG2	Landrace
20	Mesao Tssok	0.003	0.997	SG2	Landrace
21	Leikhamumei	0.001	0.999	SG2	Landrace
22	Jakherpati	0.034	0.966	SG2	Landrace
23	Machang Kaoyeng	0.011	0.989	SG2	Landrace
24	Unknown Utlou	0.002	0.998	SG2	Landrace
25	Mynri	0.001	0.999	SG2	Landrace
26	Manipur	0.003	0.997	SG2	Landrace
27	Khonemma	0.002	0.998	SG2	Landrace
28	Phouren	0.001	0.999	SG2	Landrace

29	Nagara	0.002	0.998	SG2	Landrace
30	Bhalum -4	0.001	0.999	SG2	Cultivar
31	RC Maniphou 6	0.013	0.987	SG2	Cultivar
32	RC Maniphou 7	0.002	0.998	SG2	Cultivar
33	RC Maniphou 14	0.002	0.998	SG2	Cultivar
34	RC Maniphou 15	0.002	0.998	SG2	Cultivar
35	RC Maniphou 16	0.001	0.999	SG2	Cultivar
36	KD	0.002	0.998	SG2	Cultivar
37	KD-62	0.021	0.979	SG2	Cultivar
38	RCM-22	0.003	0.997	SG2	Cultivar
39	Phoutum mah	0.998	0.002	SG1	Landrace
40	Mairong Kangbu	0.998	0.002	SG1	Landrace
41	Naga Special	0.997	0.003	SG1	Landrace
42	Mutsuku	0.999	0.001	SG1	Landrace
43	Teyang Retjang	0.998	0.002	SG1	Landrace
44	Wonder rice	0.997	0.003	SG1	Landrace
45	Haori Machang	0.988	0.012	SG1	Landrace
46	Ching chakhao	0.999	0.01	SG1	Black rice
47	ChakhaoAmubi	0.003	0.997	SG2	Black rice
48	Chakhao Lamhing	0.002	0.998	SG2	Black rice