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ARTICLE

Genetic diversity of sweet corn inbred lines of public sectors in Thailand revealed by SSR markers

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Abstract: *The Thailand governmental institutes play important roles in genetic improvement of sweet corn in Thailand. We assessed the genetic diversity of 268 sweet corn inbreds from three major institutes (NCSRC-KU, CNFCRC, and KKU) and three commercial hybrids using 20 SSR markers. The markers detected 224 alleles in total, with an average of 11.2 alleles per locus. Overall gene diversity was relatively high, being 0.7. Allelic richness, gene diversity, and heterozygosity in the inbreds among the three institutes were comparable. However, the inbreds from KKU possessed the greatest number of unique alleles and rare alleles, albeit they showed the highest percentage of genetic impurity. Neighbor-joining, principal coordinate, and STRUCTURE analyses showed that the inbreds were genetically different. Our findings provide insight into the breeding gene pool and population structures of the sweet corn germplasm of the public sector in Thailand, enhancing efficiency of sweet corn germplasm utilization for developing new varieties.*

Keywords: *Sweet corn, inbred, heterotic group, diversity, SSR marker*

INTRODUCTION

Sweet corn (*Zea mays* L. var. *saccharata* Sturt) is a variety of corn with a high sugar content grown for human consumption. Sweet corn is the result of a naturally occurring recessive mutation in some genes, for instance, *sugary-1* (*su*$_1$) *sugary enhancer* (*se*), *shrunken-2* (*sh*$_2$), and *brittle-1* (*bt*), which control conversion of sugar into starch inside the endosperm. Improved sweet corn varieties have special characteristics such as sweet taste, thin pericarp, endosperm with delicate texture, and high nutritional value (Kwiatkowski and Clemente 2007). Sweet corn can be consumed as a vegetable when harvested at the green stage, generally 20–24 days after pollination, in which the kernels have high moisture content (Khanduri et al. 2011, Mehta et al. 2017). Therefore, sweet corns for the fresh market and for freezing and canning has become an important commodity in many countries including Thailand. Thailand is a leading country in the export and production of sweet corn. In 2020, the sweet corn growing area in the country was around 38,500 hectares with a total production of 501,242 tons (Office of Agricultural Economics 2022). Thailand is the number one exporter of canned sweet corn with an export volume of 213,000 tons and amounting to a value of 216 million USD, accounting for 26.6% of the global canned sweet corn trade (Global Trade 2021).

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Continuous development of new hybrid cultivars by both governmental and private sectors has contributed greatly to the production of sweet corn in Thailand. Sweet corn breeding in Thailand was begun in 1967 by the National Corn and Sorghum Research Center of Kasetsart University (NCSRC-KU), a famous breeding institute for corn in Asia. The first sweet corn variety developed in Thailand was "Supersweet DMR" released by NCSRC-KU in 1975 (Lavapaurya et al. 1990). At present, nearly 100% of the sweet corn varieties used in Thailand are single-cross F_1 hybrids. Hybrid varieties developed by governmental institutes also contribute significantly to the sweet corn production in the country, albeit the present majority of the hybrid varieties are developed and produced by private seed companies. The first hybrid sweet corn variety in Thailand was "27127" developed by NCSRC-KU released in 1988 (Lavapaurya et al. 1990). Additional hybrid varieties of NCSRC-KU were released in short periods after that year. Inbred lines developed by governmental institutes are also used in sweet corn breeding programs by governmental and private companies for new cultivar development in Thailand and overseas. Currently, three governmental institutes, NCSRC-KU, Chai Nat Field Crops Research Center (CNFCRC), and Khon Kaen University (KKU), play important roles in the genetic improvement of sweet corn in Thailand.

In conventional breeding, inbred lines can be classified into heterotic groups by pedigree (Reid et al. 2011), morphological data (Kashiani et al. 2014), and combining ability or testcross data (the amount of heterosis expressed by the hybrid) (Kulka et al. 2018). However, these methods have several limitations. For example, pedigree analysis is often more reliable than others, but requires accurate pedigree records; however, many inbred lines are unknown pedigree. Morphological characteristics are unreliable in describing genetic relationships because all of the information is generated based on morphological characteristics that have environmental interactions. Similarly, diallel, factorial, or testcross designs have been used when the numbers of inbreds or testers are small because several inbreds or testers are extremely expensive, laborious, and time-consuming to develop. Recently, molecular markers, which provide reliable and complementary information, have been found to be more effective for characterization of inbred lines, assessment of genetic diversity, and classification of unrelated inbred lines into heterotic groups (Prasanna and Hoisington 2003). Unlike conventional classification, molecular markers are unlimited in the number of inbred lines and are not affected by environmental factors. The information provided is clear and accurate. Among the various types of markers, microsatellites or simple sequence repeats (SSRs) are considered to be one of the most suitable markers for assessing genetic diversity and assigning corn inbred lines to heterotic groups (Mahato et al. 2018) due to their high level of polymorphism, reproducibility, low cost, and amenability to automation (Govindaraj et al. 2015).

Although corn inbred lines from NCSRC-KU, CNFCRC, and KKU are widely used in breeding programs in Thailand, little is known about the genetic diversity and genetic relatedness of these inbred lines. Thus, this study is aimed at assessing the genetic diversity and heterotic grouping of 268 sweet corn inbred lines from NCSRC-KU, CNFCRC, and KKU using 20 SSR markers. The findings in this study will provide a better understanding of the gene pool diversity of corns in public sectors and enhance the efficiency of sweet corn germplasm utilization for improving and developing new sweet corn varieties in Thailand.

MATERIAL AND METHODS

Plant materials and DNA extraction

A total of 271 sweet corn genotypes were used in this study. These sweet corns included 188 inbred lines developed from CNFCRC, 39 inbred lines from KKU, 41 inbred lines from NCSRC-KU, 1 commercial F_1 hybrid from Thailand, and 2 commercial F_1 hybrids from China. The total genomic DNA of each genotype was extracted from young leaves using a modified CTAB method given by Lodhi et al. (1994). The DNA quality and quantity were assessed on 0.8% agarose gel electrophoresis by comparing with lambda DNA (Thermo Fisher Scientific, US). The DNA was adjudged to 1 ng μL^{-1} for SSR marker analysis.

SSR analysis

One hundred SSR markers covering the 10 chromosomes of maize were selected from MaizeGDB (http://www.maizegdb.org) and screened for polymorphism in five inbred lines. A polymerase chain reaction (PCR) was performed with a final reaction volume of 10 µL containing 2 ng genomic DNA, 5 pmole of each forward and reverse primer, 1× *Taq* buffer, 2 mM dNTPs, 1.5 mM $MgCl_2$, and 1 U *Taq* DNA polymerase (Thermo Fisher Scientific, US). The PCR was carried out

in a SimpliAmp Thermal Cycler (Applied Biosystems, USA). The thermal cycling profile was 94 °C for 4 min, followed by 35 cycles at 94 °C for 30 s, 50 °C for 30 s, 72 °C for 1 min, and the final extension at 72 °C for 10 min. The PCR products were separated using 5% denaturing polyacrylamide gel (w/v; 19:1 acrylamide-bisacrylamide) electrophoresis. Then the products were visualized using silver staining. Subsequently, 20 markers (two from each chromosome) showing a high number of polymorphic and clear DNA bands in the five inbred lines were further used to analyze the DNA of all samples.

Statistical analysis

The number of alleles (N_A), observed heterozygosity (H_O), gene diversity or expected heterozygosity (H_E), allelic richness (A_R), and Wright's fixation index (F_{IS}) were calculated with the SSR allele data using FSTAT program (Goudet 2002) and GenAlEx 6.5 (Peakall and Smouse 2012). The number of unique alleles (N_U) and the number of rare alleles (N_R) were counted. Rare alleles were considered as polymorphic alleles having < 1% frequency. The polymorphism information content (*PIC*) was also calculated using the SSR allele data. The outcrossing rate was then computed using the equation $t = (1 - F_{IS})/(1 + F_{IS})$ (Weir 1996). In this study, we considered the *t* value as the genetic purity.

The population structure of all inbred lines and hybrids was determined using STRUCTURE 2.3.4 (Pritchard et al. 2007). Firstly, the number of optimum *K* was estimated by conducting a 20-simulation run of the number of assumed populations (*K*) ranging from 1 to 10 and a burn-in period of 10,000 and 50,000 replicates of the Bayesian Markov Chain Monte Carlo (MCMC) algorithm. Subsequently, the number of optimum *K* was calculated using the ad hoc Δ*K* method (Evanno et al. 2005). Then STRUCTURE analysis was performed with the optimum *K* and a burn-in period of 100,000 and 500,000 replicates of the MCMC algorithm to assign each inbred line to a cluster.

To determine genetic relatedness and heterotic grouping among all inbred lines and hybrids, Nei's genetic distance (D_A) was calculated (Nei et al. 1983) using POPULATIONS 1.2.32 (Langella 2002). The D_A matrix was then utilized to cluster all the genotypes by neighbor-joining (NJ) analysis using MEGA 11.0 (Tamura et al. 2021) and principal coordinate analysis (PCoA) using R Statistical Software v4.1.2 (R Core Team 2021).

RESULTS AND DISCUSSION

SSR variation

Information regarding genetic diversity and heterotic grouping among sweet corn inbred lines has a significant impact on the utilization of germplasm to maximize the chances of obtaining hybrids expressing a high level of heterosis. In this study, we analyzed the genetic diversity and heterotic grouping of 268 sweet corn inbred lines from CNFCRC, KKU, and NCSRC-KU, the three main public institutes having strong breeding programs of sweet corns using 20 SSR loci across the 10 maize chromosomes (2 SSRs from each chromosome). A total of 224 alleles were detected with the number of alleles per locus (N_A) ranging from 5 (markers umc1123, umc1394 and umc1276) to 20 (marker bnlg1033) with an average of 11.2 (Table 1). The average number of alleles per locus in our sweet corns was much higher than that in sweet corn germplasms previously reported by Ko et al. (2016) (1.96 alleles per locus from 50 SSRs in 87 diverse sweet corn inbreds conserved in a public institute of Korea), by Mehta et al. (2017) (3.8 alleles per locus from 56 SSRs in 48 diverse sweet corn genotypes from *su1su1*, *sh2sh2*, and s*u1su1/sh2sh2* types of public institute of India), and by Ferreira et al. (2018) (3.85 alleles per locus

Table 1. Number of alleles (N_A), observed heterozygosity (H_O), gene diversity (H_E), polymorphism information content (*PIC*) of 268 sweet corn inbred lines, and three F_1 hybrids detected by 20 SSR markers

Markers	Chromosome	N_A	H_O	H_E	*PIC*
umc1123	1	5	0.085	0.352	0.35
umc1128	1	16	0.405	0.835	0.83
umc1042	2	12	0.142	0.601	0.59
umc1823	2	14	0.098	0.849	0.85
bnlg197	3	14	0.138	0.867	0.86
umc1394	3	5	0.082	0.639	0.64
nc004	4	10	0.113	0.829	0.83
umc1276	4	5	0.097	0.676	0.67
umc1155	5	14	0.099	0.606	0.60
umc1225	5	16	0.079	0.818	0.81
bnlg1617	6	17	0.141	0.856	0.85
nc013	6	11	0.055	0.823	0.82
umc1125	7	6	0.104	0.531	0.53
umc1393	7	9	0.106	0.717	0.71
umc1034	8	12	0.147	0.841	0.84
umc2210	8	7	0.104	0.735	0.73
bnlg1724	9	19	0.178	0.798	0.80
umc1033	9	20	0.111	0.892	0.89
umc1061	10	6	0.064	0.356	0.36
umc1380	10	6	0.140	0.604	0.60
Average	-	11.2	0.124	0.710	0.71
Overall	-	224	0.125	-	-

from 20 SSRs in 12 sweet corn inbreds of an elite line group of the Maringá State University (Brazil) and Syngenta Seeds Ltd.). Nonetheless, the high number of alleles and alleles per locus in our study indicates wide genetic variation among the sweet corn inbred lines in the public sectors in Thailand. The high genetic diversity detected in the public sectors allows the development of promising divergent inbred lines and hybrid varieties.

The *PIC* values of the SSR loci varied from 0.35 for umc1123 to 0.89 for bnlg1033 with an average of 0.71 (Table 1). A high average PIC value of the SSR markers used in our study suggests that those markers have high discriminatory power for genetic diversity studies and grouping of genotypes into different groups.

Genetic diversity in the sweet corn inbreds

The number of alleles (N_A), number of unique alleles (N_U), number of rare alleles (N_R), allelic richness (A_R), observed heterozygosity (H_O), gene diversity (H_E), fixation index (F_{IS}), and outcrossing rate (t) of the inbred lines from the three public institutes of Thailand are summarized in Table 2. N_A varied from 117 in NCSRC-KU to 162 in KKU with an average of 143.33. In this study, a high N_U (77 alleles or 34.8%) were identified by 18 SSR loci. N_U varied from 16 in NCSRC-KU to 31 in KKU with an average of 25.67. However, N_U in KKU was nearly the same as that in CNFCRC. Similarly, a high N_R (65 alleles or 29.4%) were identified. N_R varied between 14 in NCSRC-KU and 30 in KKU with an average of 21.67. A_R varied between 115.67 in NCSRC-KU and 159.78 in KKU with an average of 133.44. The high numbers of N_U and N_R also indicate high genetic base of the sweet corn inbreds in the public sectors in Thailand. Unique and rare alleles are useful for identification of inbred lines in the Thai sweet corns and their derivatives. Additionally, they may be associated with specific traits (Muthusamy et al. 2015), albeit further studies are necessary to clarify the association between these alleles and phenotypic traits. Although the N_U and N_R depends upon the number of germplasms analyzed, the inbred lines from KKU possessed the greatest N_U and N_R, especially the latter, in spite of their line number being lesser than those from CNFCRC and NCSRC-KU. It is worth noting that the number of inbred lines from KKU was only 39. They had 31 unique and 30 rare alleles; thus nearly every single individual possessed unique and rare alleles. However, it is noteworthy that the lines from KKU showed high H_O (21% (Table 2), indicating that a large portion of the alleles have not yet been fixed. The same is true for the lines from NCSRC-KU where the H_O was 11% (Table 2). Nonetheless, the high N_U and N_R in the sweet corn germplasm of the KKU are valuable for public corn breeding in Thailand.

SSR markers are co-dominant and are thus useful in detecting heterozygosity among the inbred lines. In this study, the overall H_O in the 268 inbred lines was as high as 0.13. As mentioned before, the H_O in the KKU and NCSRC-KU inbred lines was very high, and a result was not expected for inbred line(s). Ferreira et al. (2018) reported 0.08 heterozygosity residues in 12 elite sweet corn inbred lines from public universities and private companies (Syngenta Seeds Ltd.). The markers umc1128 and bnlg1724 revealed high heterozygosity of 0.405 and 0.178, respectively (Table 1). Our inspection found that at these two markers, the heterozygosity was high in the inbred lines—0.51 for KKU, 0.392 for NCRSC-KU, and 0.316 for CNFCRC at umc1128 and 0.404 for KKU, 0.075 for NCRSC-KU, and 0.053 for CNFCRC at bnlg1724. Though corn inbreds tend to segregate for a few loci regardless of the repeated cycles of controlled self-pollination over many generations (Kaur et al. 2011) and high heterozygosity at some loci could be attributed to the residual heterozygosity (Mahato et al. 2018), the high heterozygosity at umc1128 and bnlg1724 is unusual. It is possible that heterozygosity at these loci may provide phenotypic advantage(s) for several inbred lines through dominant and over-dominant gene effect, and the heterozygosity is maintained through selection of such phenotype(s) during inbred line development. Nonetheless, due to the high residual heterozygosity observed in the KKU and NCSRC-KU inbred lines, more stringent

Table 2. Number of alleles (N_A), number of unique alleles (N_U), number of rare alleles (N_R), allelic richness (A_R), observed heterozygosity (H_O), gene diversity (H_E), fixation index (F_{IS}), and outcrossing rate (t) in 268 sweet corn inbred lines from CNFCRC, KKU, and NCSRC-KU detected by 20 SSR markers

Source	Number of individuals	N_A	N_U	N_R	A_R	H_O	H_E	F_{IS}	t (%)
CNFCRC	188	151	30	21	124.87	0.06	0.65	0.92	4.33
KKU	39	162	31	30	159.78	0.21	0.72	0.72	16.55
NCSRC KU	41	117	16	14	115.67	0.11	0.66	0.84	8.87
Overall	268	221	77	65	165.39	0.13	0.71	0.88	6.44
Average	89.33	143.33	25.67	21.67	133.44	0.12	0.68	0.82	9.92

practices and additional self-pollinations must be performed to obtain higher genetically uniform inbred lines from these two institutes.

The overall gene diversity (H_E) in the 268 inbred lines was relatively high, being 0.71. The H_E among the different institutes was comparable, varying between 0.65 and 0.72. The gene diversity computed for the 268 sweet corn inbreds is likely to be overestimated, as stated before, due to unusual high residual heterozygosity at some loci, and thus, conclusion regarding genetic diversity in the sweet corns of public sectors in Thailand must be interpreted with caution. However, the gene diversity found in our sweet corns (0.71) was comparable to that found in 12 inbreds (0.64) reported by Ferreira et al. (2018) and in 87 inbreds reported by Ko et al. (2016).

The overall F_{IS} was 0.88, while the overall genetic impurity (t) was 6.44%. The inbred lines from KKU showed the highest genetic impurity (16.55%), about two- and four-fold higher than those from NCSRC-KU and CNFCRC, respectively. The percentage of genetic purity of the inbred lines is an important genetic parameter in corn hybrid breeding and production. Our results suggest that additional rounds of self-pollination must be performed for the inbred lines from KKU.

Cluster analysis

Genetic admixture (population structure) of the 271 corn germplasms was determined using the STRUCTURE software. The ad hoc ΔK analysis (Evanno et al. 2005) clearly showed the peak at K = 2 (Figure S1) and suggested that there were two subpopulations, I and II, in the 271 sweet corn inbred lines and hybrids (Figure 1). Based on the STRUCTURE analysis, subpopulation I consisted of 78 inbred lines comprising 4 from CNFCRC, 34 from KKU, and 40 from NCSRC-KU. The three hybrids were also categorized in subpopulation I (Figure 1 and Table S1). On the other hand, subpopulation II consisted of 190 inbred lines containing 184 from CNFCRC, 5 from KKU, and 1 from NCSRC-KU (Figure 1 and Table S1).

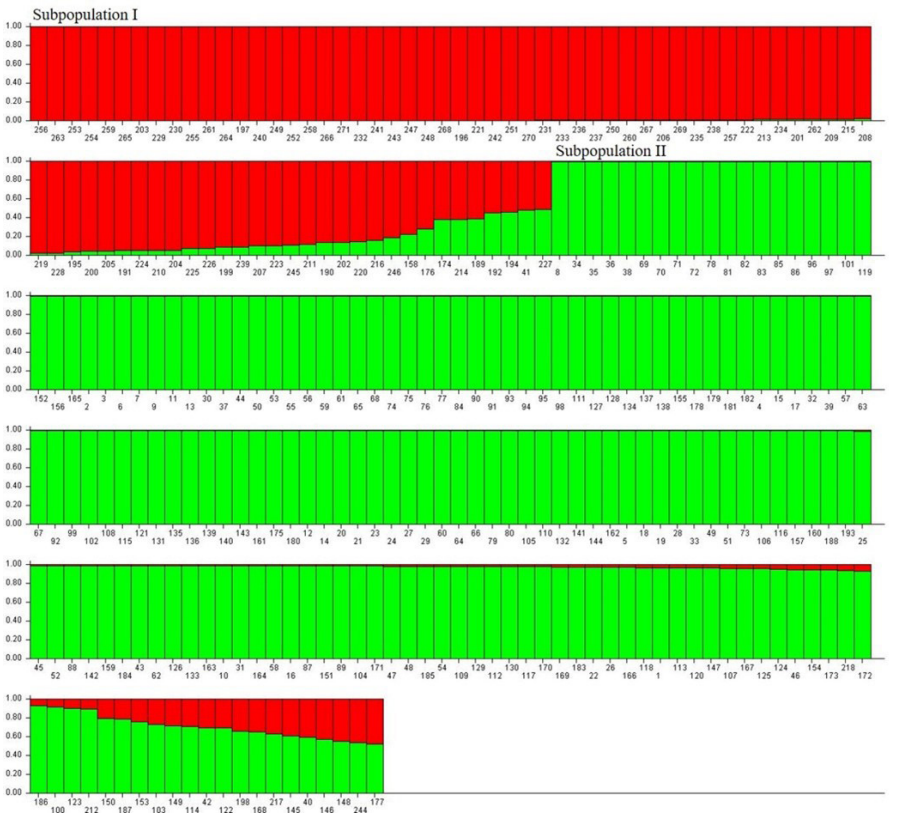

Figure 1. Two subpopulations of the 271 sweet corn inbred lines and hybrids determined using STRUCTURE analysis based on allelic data of 20 simple sequence repeat loci. Each bar represents one accession.

A neighbor-joining (NJ) tree of the 271 sweet corn inbred lines and hybrids was constructed using Nei's genetic distance. The tree showed that the sweet corn inbred lines and hybrids were grouped into two major clusters (I and II) (Figure 2A). Cluster I was composed of 62 inbred lines from all institutes and the three hybrid cultivars. This cluster could be separated into three sub-clusters, I-A, I-B, and I-C (Figure 2A). The sub-cluster I-A mainly contained inbred lines from NCSRC-KU (18 inbred lines) and some from CNFCRC (5 inbred lines) and KKU (3 inbred lines). The sub-cluster I-B contained 15 inbred lines from NCSRC-KU and the three hybrids. The sub-cluster I-C contained 1, 12, and 8 inbred lines from CNFCRC, KKU, and NCSRC-KU, respectively. Cluster II was composed of six sub-clusters (II-A, II-B, II-C, II-D, II-E, and II-F) that contained 206 inbred lines from CNFCRC and KKU. The sub-clusters II-A, II-B, and II-C purely contained inbred lines from CNFCRC, while II-D contained all except one inbred line from CNFCRC. The sub-clusters II-E and II-F contained all inbred lines from CNFCRC. Interestingly, all of the inbred lines from NCSRC-KU were clustered together in cluster I, while almost all of inbred lines from CNFCRC were clustered together in cluster II and the inbred lines from KKU were distributed in both clusters (Figure 2A). When the information from clustering based on STRUCTURE analysis was

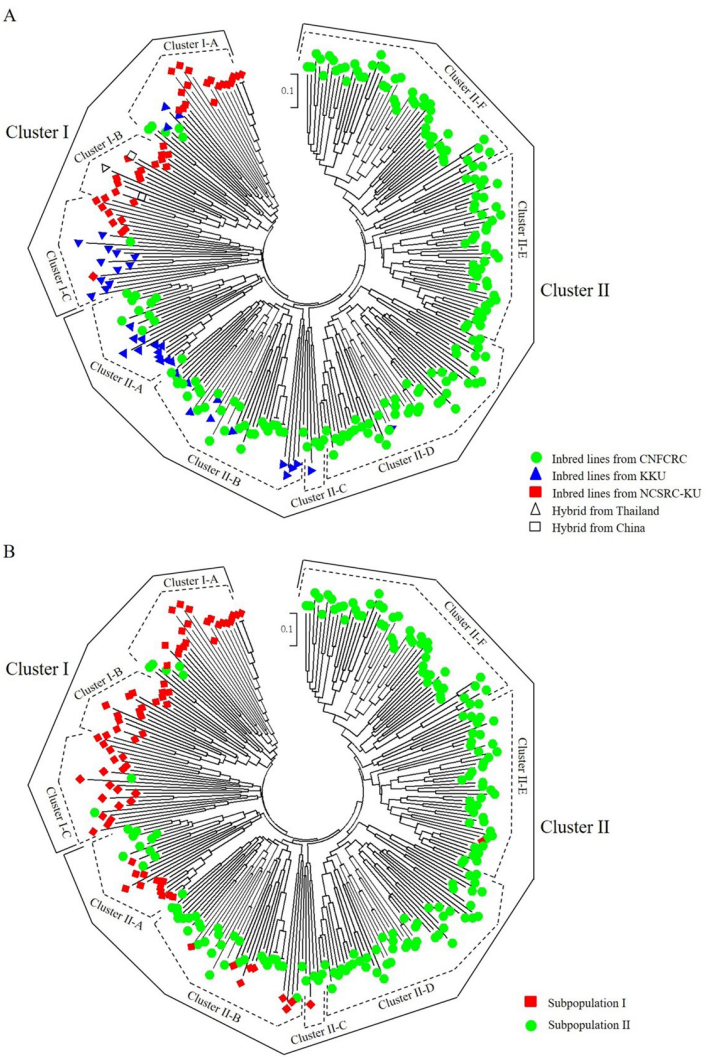

Figure 2. Neighbor-joining tree depicting genetic relationship among the 268 sweet corn inbred lines and three hybrid varieties based on allelic data of 20 simple sequence repeat loci. (A) Individuals are shown based on their sources of origin. (B) Individuals are shown based on subpopulations they belong to as determined by STRUCTURE analysis.

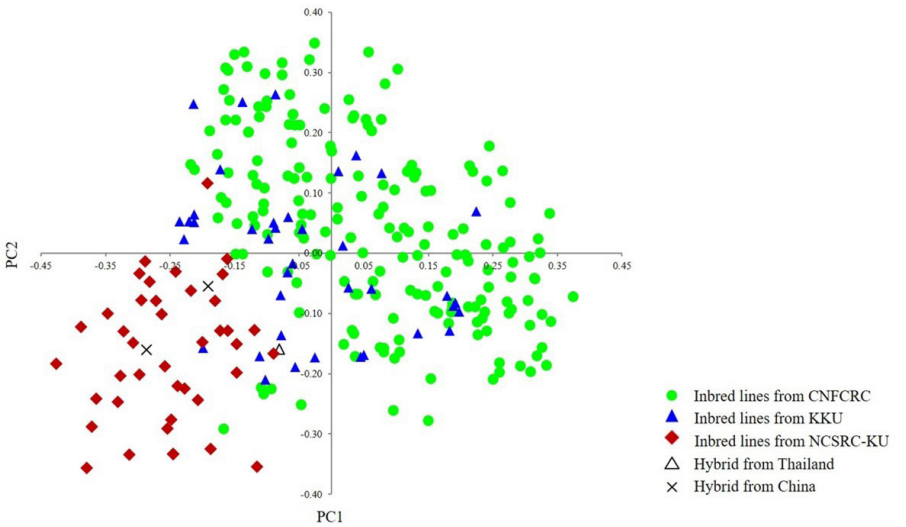

Figure 3. A biplot (PC1 and PC2) from principal coordinate analysis showing genetic relationship among 268 sweet corn inbred lines and three hybrid varieties based on allelic data of 20 simple sequence repeat loci.

integrated into the NJ tree (Figure 2B), most of the inbred lines belonging to subpopulation I was clustered together. Similarly, most inbred lines belonging to subpopulation II were also grouped.

PCoA analysis based on Nei's genetic distance revealed that the first two PCs, PC1 and PC2, showed 11.21% and 8.68% of the total variation, respectively. Based on the two PCs, a PCoA plot of 271 sweet corn germplasms revealed that the inbred lines were distributed in all four quadrangles. The inbred lines from NCSRC-KU were on the bottom left of the plot and clearly separated from the inbred lines from CNFCRC (Figure 3), whereas the inbred lines from KKU showed overlapped distribution with inbred lines from CNFCRC (Figure 3).

Population structure is important for understanding and explaining the heterogeneity of genetic architecture and is mainly affected by gene exchange (Huang and Feldman 2017). In this study, clustering of all the sweet corn inbred lines from the three different sources using STRUCTURE analysis, NJ analysis, and PCoA generally gave similar results that inbred lines were clearly clustered into two major clusters (Figures 1-3). The similar results among the different analytical methods suggest the high reliability of the clustering. The clear differentiation between inbred lines from NCSRC-KU and those from CNFCRC (Figures 2A and 3) may indicate different genetic bases, breeding strategies (selection methods), and target traits in the breeding programs in these two institutes. It also indicates a low germplasm exchange between the institutes. Low genetic exchange and restrictions on germplasm access negatively impact plant breeding and agricultural production (Smith et al. 2021). The results from the cluster analysis (Figures 2A and 3) suggest that KKU inbred lines are likely to be derived from sweet corns of NCSRC-KU and CNFCRC. In addition, a Thai commercial hybrid and two Chinese hybrids were grouped with a subgroup of NCSRC-KU inbred lines (Figures 2A and 3). This result suggests a narrow genetic base of the sweet corn hybrids available in Thailand, albeit only a small number of hybrids were used in this study. Therefore, the information on the relationships among sweet corn inbred lines in this study will be helpful to sweet corn breeders for the exploitation of germplasm and planning crosses for hybrid production. Specifically, the inbred lines belonging to clusters I and II may be useful in cross combinations with each other.

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