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Characterization of Kenyan French Bean genotypes into gene pool affiliations using allele specific markers

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French bean (Phaseolus vulgaris L.) is a major export crop in Kenya where it serves as a cash crop for smallholder farmers and a source of employment. However, there is limited information on characterization of available germplasm which is essential in genetic improvement of this crop. The present study was therefore aimed to identify the gene pool affiliations of Kenyan French bean germplasm using specific molecular markers in order to understand the available germplasm for future use in breeding programs. The germplasm panel consisted of 46 accessions, comprising 40 French bean and six dry bean genotypes. The accessions were characterized using four gel-based molecular markers: SHP1-A, SHP1-B, SHP1-C and phaseolin protein marker. The most informative marker was the phaseolin protein marker which indicated that 82% of the French bean genotypes are of Andean origin, while 18% are of the Mesoamerican origin. Low polymorphism was observed for the SHP1 markers and the data from the three SHP1 markers did not correspond to the phaseolin protein marker for the French bean germplasm although SHP1-A and SHP1-B were able to differentiate the Andean from the Mesoamerican differential cultivars. The information on the gene pool affiliations of Kenyan French bean accessions is important for breeders to harness the divergence between the two gene pools in order to broaden the genetic base of the crop.

Key words: Gene pool, phaseolin protein, shatterproof, molecular markers, French beans.

INTRODUCTION

French beans designate common beans (Phaseolus vulgaris L.) with flesher immature pods that are consumed as a vegetable (Singh and Singh, 2015; Myers and Kmiecik, 2017). The crop is a major export vegetable in Kenya although production has not matched its yield potential due to institutional challenges and a number of biotic and abiotic constraints. French bean breeding efforts in eastern Africa have mainly focused on pod yield improvement, local adaptation and incorporating disease resistance into contemporary cultivars (Wasonga et al., 2010; Wahome et al., 2011). Despite the breeding efforts in Kenya, cultivar release has been slow partly due to the limited understanding of the available germplasm. Few studies have attempted to characterize French bean

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germplasm in Kenya (Arunga et al., 2015). There is therefore a need for more studies on French bean germplasm because successful plant-breeding programs depend on characterizing genetic diversity in order to identify parents to be used as sources of breeding stocks.

The domestication of the common bean has the Mesoamerican and Andean gene pools (Beebe et al., 2001). The classification of these gene pools was according to phaseolin seed protein (Gepts and Bliss, 1988), different allozymes (Singh et al., 1991), nucleotide sequences (McCLean and Lee, 2007; Nanni et al., 2011) and a number of molecular markers (Acosta-Gallegos et al., 2007; Papa et al., 2006). Worldwide, genetic diversity among French bean germplasm has been conducted based on multilocus molecular markers (Kwak and Gepts, 2009; Wallace et al., 2018). Previously, French beans were grouped as of the Andean origin (Singh et al., 1991), but later reports have grouped them in both gene pools of common bean depending on the region of collection (Blair et al., 2010; Wallace et al., 2018). Hybridization between the two gene pools have also been reported (Cunha et al., 2004).

The earliest studies of variations in common bean were based on the phaseolin protein (Gepts et al., 1986). This protein plays an essential role as a molecular marker in the understanding of common bean gene pools and genetic diversity analyses (Gepts and Bliss, 1988; Singh, 2001). These phaseolin diversity studies have been achieved under denaturing conditions through some procedures such as sodium dodecyl sulphate (SDS) polyacrylamide gel electrophoresis or mass spectrometry (De La Fuente et al., 2012). Kami et al. (1995) developed a gel-based co-dominant SCAR marker that was able to discriminate between the two gene pools of common beans in an easy, fast and reliable process. The marker has been useful in understanding the common bean germplasm and also for marker-assisted selection for quantitative trait loci (QTL) conferring partial resistance to white mold in dry bean (Miklas, 2007; De la Fuente et al., 2012). In addition, Nanni et al. (2011) developed sequence tagged site (STS) markers that can be used to distinguish Mesoamerican and Andean gene pools. The three polymerase chain reaction (PCR) -based indel spanning markers (SHP1-A, SHP1-B, and SHP1-C) were designed based on PvSHP1 gene sequences in common bean, a genomic sequence that is homologous to SHATTERPROOF-1 (SHP1) of A. thaliana. The PvSHP1 in common bean is linked to the V locus for flower color and is a genomic region where QTLs for days to flowering and common bacterial blight resistance have been mapped (Blair et al., 2006; Miklas et al., 2006). The PvSHP1 sequence is highly polymorphic and it has been particularly useful in distinguishing Mesoamerican and Andean gene pools (Angioi et al., 2010; Nanni et al., 2011; Pipan and Meglic, 2019). The present study was therefore aimed at characterizing Kenyan French bean germplasm into affiliated gene pools in order to understand the material for future use in breeding programs.

MATERIALS AND METHODS

Plant material
The studied plant material was made up of 46 accessions, comprising 40 French bean accessions (designated FBK1-40) and six dry bean cultivars: Pan 72, G5686, BAT 332, G11796, Mex 54 and G2333 (Table 1). The French bean accessions comprised of 32 commercial French bean varieties (obsolete and current), five breeding lines and three landraces. The French bean seeds were obtained from farmers, various research organizations and seed distributors in Kenya, while the landraces were obtained from the National gene bank of Kenya. Seed for the differentials was sourced from the International Center for Tropical Agriculture, Uganda. The gene pools of the differential cultivars are known (Liebenberg and Pretorius, 1997) and included in the study as controls.

DNA analysis
Plants used for DNA extraction were planted in a greenhouse maintained at 25±5°C at the University of Embu, Kenya. Leaves were collected from three-week old plants and DNA was extracted using the Muhlku DNA extraction protocol (Muhlku, 2004). PCR amplification used three STS markers: SHP1-A, SHP1-B, SHP1-C (Nanni et al., 2011) and the Phaseolin protein SCAR (Kami et al., 1995) (Table 2). The PCR reactions were composed of a total reaction volume of 10 μl in FrameStar® Break-A-Way PCR tubes containing 1X Dream Taq buffer (containing 2 mM MgCl₂), 0.2 mM dNTPs, 0.5 μM of each reverse and forward primers, 0.1U Taq Polymerase (Thermo Fisher Scientific) and 5 ng/μl of genomic DNA. The DNA was amplified using the following thermocycler regime: an initial denaturation step at 94°C for 3 min; followed by 35 cycles of the following three steps: denaturation at 94°C for 10 s, annealing for 40 s, an extension at 72°C for 2 min; and a final extension step at 72°C for 5 min. The annealing temperatures for each marker are shown in Table 2. After amplification, a volume of 2 μl of 6× DNA loading dye (NEB) was added to each PCR reaction. The contents were loaded in 0.25% agarose gel pre-stained with 5 μM Etidium bromide in 1X Sodium borate buffer and run at 100 volts at 3 h. For confirmation, a repeat of electrophoresis was done using 6% non-denaturing polyacrylamide gel, run horizontally at 100 V for 3 h, before staining with ethidium bromide. The DNA bands were viewed under ultraviolet light (UVP® GelDoc-it system). The major allele frequency, number of alleles per locus, gene diversity and polymorphic information content (PIC) were determined using Power Marker version 3.25 (Liu and Muse, 2005). Genetic distances among the 46 accessions were calculated using the Jaccard distance measure and the unweighted paired group method with arithmetic mean (UPGMA) tree was constructed using DARwin version 6.0.021 (Perrier and Jacquemoud-Collet, 2006).

RESULTS
All the four markers successfully amplified the 46 accessions revealing a mean of 2.25 alleles (Table 3). The most informative marker was the phaseolin protein SCAR marker with the polymorphism information content (PIC) value of 0.33. The phaseolin protein SCAR marker
### Table 1. Description of germplasm under study.

| S/N | Accession name | Cultivar class  | Gene pool         |
|-----|----------------|-----------------|-------------------|
| 1   | FBK1           | Obsolete commercial | Undesignated     |
| 2   | FBK2           | Current commercial | Undesignated     |
| 3   | FBK3           | Breeding line    | Undesignated     |
| 4   | FBK4           | Breeding line    | Undesignated     |
| 5   | FBK5           | Obsolete commercial | Undesignated     |
| 6   | FBK6           | Breeding line    | Undesignated     |
| 7   | FBK7           | Breeding line    | Undesignated     |
| 8   | FBK8           | Current commercial | Undesignated     |
| 9   | FBK9           | Current commercial | Undesignated     |
| 10  | FBK10          | Breeding line    | Undesignated     |
| 11  | FBK11          | Current commercial | Undesignated     |
| 12  | FBK12          | Current commercial | Undesignated     |
| 13  | FBK13          | Current commercial | Undesignated     |
| 14  | FBK14          | Current commercial | Undesignated     |
| 15  | FBK15          | Gene bank landrace | Undesignated     |
| 16  | FBK16          | Current commercial | Undesignated     |
| 17  | FBK17          | Gene bank landrace | Undesignated     |
| 18  | FBK18          | Current commercial | Undesignated     |
| 19  | FBK19          | Current commercial | Undesignated     |
| 20  | FBK20          | Current commercial | Undesignated     |
| 21  | FBK21          | Obsolete commercial | Undesignated     |
| 22  | FBK22          | Gene bank landrace | Undesignated     |
| 23  | FBK23          | Current commercial | Undesignated     |
| 24  | FBK24          | Current commercial | Undesignated     |
| 25  | FBK25          | Current commercial | Undesignated     |
| 26  | FBK26          | Obsolete commercial | Undesignated     |
| 27  | FBK27          | Current commercial | Undesignated     |
| 28  | FBK28          | Current commercial | Undesignated     |
| 29  | FBK29          | Current commercial | Undesignated     |
| 30  | FBK30          | Current commercial | Undesignated     |
| 31  | FBK31          | Current commercial | Undesignated     |
| 32  | FBK32          | Current commercial | Undesignated     |
| 33  | FBK33          | Current commercial | Undesignated     |
| 34  | FBK34          | Current commercial | Undesignated     |
| 35  | FBK35          | Current commercial | Undesignated     |
| 36  | FBK36          | Current commercial | Undesignated     |
| 37  | FBK37          | Current commercial | Undesignated     |
| 38  | FBK38          | Current commercial | Undesignated     |
| 39  | FBK39          | Current commercial | Undesignated     |
| 40  | FBK40          | Current commercial | Undesignated     |
| 41  | Pan 72         | ALS differential  | Mesoamerican      |
| 42  | G05686         | ALS differential  | Andean            |
| 43  | BAT 332        | ALS differential  | Mesoamerican      |
| 44  | G11796         | ALS differential  | Andean            |
| 45  | Mex 54         | ALS differential  | Mesoamerican      |
| 46  | G2333          | Anthracnose differential | Mesoamerican      |

(Phs) amplification produced two major profiles across the 46 entries. The first one consisting of two fragments of 249 and 270 bp and was considered of the Mesoamerican gene pool, and the second one contained
three fragments of 249, 264 and 285 bp, and was considered of the Andean gene pool (Figure 1). Based on the phaseolin protein markers, 82% of the French bean genotypes are of Andean origin while 18% are of the Mesoamerican origin. Further, the Mesoamerican differentials produced two fragments of 249 and 270 bp while the Andean differential cultivars contained three fragments of 249, 264 and 285 bp.

The PIC values for SHP1 markers were very low with SHP1-B having the highest value (0.17). The data from the three SHP1 markers did not correspond to the phaseolin protein marker results for the French bean germplasm. However, SHP1-A and SHP1-B were able to differentiate the Andean differential cultivars (G5686 and G11796) from the Mesoamerican (G2333, Mex 54, Pan 72 and BAT 332) differential cultivars. For SHP1-A, the Andean differential cultivars had the 206 bp allele while the Mesoamerican differentials had the 198 bp, while for SHP1-B the Andean differential cultivars had the 211 bp allele while the Mesoamerican differentials had the 221 bp (Figure 2). Only three French bean accessions (FBK20, 26 and 38) were different from the rest when amplified with SHP1-A and SHP1-B. Furthermore, SHP1-C was monomorphic for all the accessions except for three French bean accessions. Majority of the accessions possessed the 127 bp band while FBK 3, 7 and 38 possessed the 119 bp band.

Cluster analysis grouped the 46 accessions into three major clusters (Figure 3). Cluster I was made up of 29 French bean accessions which showed no variability for the three markers. These accessions were grouped as Andean genotypes using the phaseolin seed storage protein marker. Cluster II was made up of 5 breeding lines (1, 3, 4, 7, 10) one obsolete commercial cultivar (21) and a landrace (22). These group was classified as of Mesoamerican gene pool based on the phaseolin protein marker. However, they showed no polymorphism for the SHP markers. Cluster III was made up of the differential cultivars (42, 44) and three French bean accessions (20, 26, 38) that were polymorphic for SHP-A and SHP-B markers. The members of the third cluster were classified to be of Andean origin based on the phaseolin protein marker.

**DISCUSSION**

The phaseolin seed storage protein is an important molecular marker in common bean (Carović-Stanko et al. 2017). This marker has been used to characterize common bean genotypes in East Africa (Tanzania and Uganda) recording the predominance of Andean genotypes as compared with the Mesoamerican genotypes (Okii et al., 2014; Chilagane et al., 2016). In Europe the phaseolin protein marker, together with SHP1 markers, were able to successfully indicate the gene pool
Figure 1. PCR amplification products of genomic DNA from *P. vulgaris* L. genotypes amplified with Phs SCAR marker electrophoresed on 1.5% agarose gels. Ld = 50 bp ladder, 8 = FBK8, 9 = FBK9, 10 = FBK10, 11 = FBK11, 12 = FBK12, 13 = FBK13, 14 = FBK14, 15 = GBK FBK15, 16 = FBK16, 17 = FBK17, 18 = FBK18, 19 = FBK19, 20 = FBK20, 21 = FBK21, 22 = FBK22, 23 = FBK23, 24 = FBK24, 25 = FBK25.

Figure 2. PCR amplification products of genomic DNA from *P. vulgaris* L. genotypes amplified with SHP1-B electrophoresed on 1.5% agarose gels. Ld = 100 bp ladder, 14 = FBK14, 15 = GBK FBK15, 16 = FBK16, 17 = FBK17, 18 = FBK18, 19 = FBK19, 20 = FBK20, 21 = FBK21, 22 = FBK22, 23 = FBK23, 24 = FBK24, 25 = FBK25, 26=FBK26, 39 = FBK39, 45= Mex 54, 41 = PAN 72, 42 = G05686, 43 = BAT 332.

origins of common bean germplasm from various parts of Europe (Pipan and Meglic, 2019). In contrast, the information obtained from the three SHP1 markers in this study was not enough to categorize the French bean
Figure 3. UPGMA dendrogram illustrating genetic similarities of 40 French bean accessions and six dry bean genotypes based on analysis of four gene pool specific markers using Jaccard distance.

germplasm into specific gene pools. The SHP1 markers were only useful in subdividing the Andean gene pool further which were already classified using the phaseolin protein marker. The phaseolin protein marker is therefore useful in classifying the French bean accessions into gene pools.

SHATTERPROOF (SHP) belongs to the family of MADS-box genes and is involved in fruit shattering in *Arabidopsis* (Liljegren et al., 2000). In common bean, pod dehiscence is characterized by the presence of pods suture strings and wall fibers (Singh and Singh, 2015). Koinange et al. (1996) mapped the *St* gene, which is responsible for the presence or absence of pod string, on linkage group Pv02. Hagerty et al. (2016) recorded a QTL for string: pod length (PL) ratio found on Pv02 in a dry bean × snap bean mapping population. However, Davis et al. (2006) located a QTL on Pv06 for pod strings using a mapping population involving two snap beans, suggesting that there may be additional loci for pod suture strings. Nanni et al. (2011) reported that the *PvSHP1* fragment did not map to the *St* gene (the *PvSHP1* was mapped on PV06) although the authors could not totally exclude that the *PvSHP1* is somewhat involved in genetic control of fruit shattering in *Phaseolus*.

In this regard, further studies are recommended using a diverse and large French bean germplasm pool to understand the low polymorphism of the SHP1 markers in French beans. Contemporary French bean cultivars are stringless and lack pod fibers and this could be the reason for lack of variability when using the SHP1 markers.

The predominance of Andean gene pool among French bean genotypes has been reported previously (Metais et al., 2002; Wallace et al., 2018). In the present study, the predominance of the Andean gene pool was evident supporting the studies by Arunga et al. (2015) who characterized Kenyan French beans using microsatellite markers. The few entries that were classified as Mesoamerican were either landraces or breeding lines. The breeding lines were obtained from one breeding program, which utilized resistance genes from both gene pools (including dry beans). All commercial French bean cultivars are of Andean origin indicating the narrow genetic base of the commercial cultivars.

The consequence of having predominance to the Andean gene pool among French beans is the low diversity that exists among the Andean gene pool and their susceptibility to major pathogens in East Africa.
Studies on common bean diseases have reported an association of plant pathogens with the common bean gene pool. Chilagane et al. (2016), while studying the interaction between the common bean host and Pseudocercospora griseola, found out that Andean genotypes were more susceptible compared with Mesoamerican genotypes. Similar studies on rust (Uromyces appendiculatus), angular leaf spot (ALS) and anthracnose (Colletotrichum lindemuthianum) in Kenya point towards the importance of using the Mesoamerican gene pool as sources of resistance (Arunga et al., 2012; Mogita et al., 2013; Kimno et al., 2016). The challenge of inter-genepool hybridization is the low success rate of transferring important quantitative traits from one gene pool to another (Johnson and Gepts, 1999). This has been observed especially in French beans where the French bean pod traits are usually affected. Breeders can therefore diversify the germplasm by collecting host plants from locations with high disease or with high pathogen diversity as recommended by Acevedo et al. (2008). Crosses within the same gene pool have been the most effective strategy to improve yield, adaptability and resistance to diseases in common bean (Kelly et al., 1998). In situations where this is not possible, French bean breeders can cross between the two gene pools using appropriate selection methods in combination with molecular markers to increase selection efficiency.

Conclusion

This study has revealed that most commercial French bean varieties grown in Kenya are of Andean origin and therefore breeders can harness the divergence between the two gene pools to broaden the genetic base of the crop. Furthermore, the phaseolin protein marker has shown to be informative for determination of the gene pool affiliations of Kenyan French bean accessions. Further studies are recommended on germplasm characterization using the SHP1 markers in a diverse and large French bean germplasm pool.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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