INTEGRATING PHENOTYPIC EVALUATIONS WITH A MOLECULAR DIVERSITY ASSESSMENT OF AN ETHIOPIAN COLLECTION OF COMMON BEAN LANDRACES

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ABSTRACT

Understanding the organisation of genetic diversity in a crop species is a key element for both the conservation and utilisation of its genetic resources. In the case of common bean (*Phaseolus vulgaris* L), Ethiopia is one of the secondary centers of diversity of this species. Hence, this study sought to improve our understanding of genetic diversity of common bean by integrating morphological and agronomic evaluations with prior molecular diversity data from a collection of landrace accessions from different common bean growing regions of Ethiopia. The samples studied included 115 landraces, four standard varieties, and two control genotypes. Twenty agronomic traits and morphological descriptors were used to evaluate the accessions under field conditions. A Principal Component Analysis clearly separated the accessions into the Andean and Mesoamerican gene pools, with the first two axes explaining most of the variation. Step-wise discriminant and canonical correlation analyses, with all variables or only the morphological variables, enabled the identification of characters distinguishing accessions from the Andean/Mesoamerican gene pools, and their respective ecogeographic races. Data distinguishing racial and morphological traits were used to clarify the identities of five cluster groups, identified at STRUCTURE preset K = 5, in a preceding study. The three Andean cluster groups were shown to belong to two of the races in the gene pool, 'Nueva Granada' and 'Peru'; while the two Mesoamerican groups were from the race 'Mesoamerica'. By integrating the morphological and agronomic evaluation of an Ethiopian germplasm collection of common bean, initially performed just based on molecular characterisation, we were able to improve our understanding of the organisation of this diversity. Our results suggest extensive hybridisation between the Andean and Mesoamerican gene pools after introduction of common bean germplasm in Ethiopia.

Key Words: Canonical discriminant analysis, genetic resources, intra-specific diversity, multivariate analyses, plant breeding, principal component analysis

RÉSUMÉ

Connaitre l'organisation de la diversité génétique sur une culture est un élément important à la fois pour la conservation et l'utilisation de ses ressources génétiques. Dans le cas du haricot commun (*Phaseolus vulgaris* L), l'Ethiopie est l'un des centres secondaires de la diversité de l'espèce. Par conséquent, cette étude cherche à améliorer notre compréhension de la diversité génétique du haricot commun en intégrant les évaluations morphologique et agronomiques avec une évaluation préalable de la diversité moléculaire d'une collection de cultivars traditionnels venus de différentes régions productrices du haricot commun de l'Ethiopie. Les échantillons utilisés comprennent 115 cultivars traditionnels, quatre variétés standards, et deux génotypes contrôles. Vingt traits descripteurs agronomiques et morphologiques étaientutilisés pour évaluer les accessions dans des conditions de champ. Une analyse en composante principale a clairement séparé les accessions en des pools de gènes Andins et Mésoaméricains avec les deux premiers axes expliquant la plus grande variation. Les analyses discriminante par étapes la corrélation canonique, avec toutes les variables ou seule avec les variables morphologiques, ont permis l'identification des caractères discriminant les accessions des pools de gènes Andins et Mésoaméricains, et leurs races Eco géographiques respectives. Les données discriminant les traits raciaux et morphologiques étaient utilisés pour clarifier les identités des cinq classes, identifiées à la configuration préfinie K= 5, dans l'étude précédente. Les trois groupes de classes Andines appartiennent à deux races dans le pool de gènes, 'Nueva Granada' et 'Peru' ; alors que les groupes Mésoaméricains étaient de la race 'Mésoamérica'. En intégrant l'évaluation morphologique et agronomique de la collection du germplasm du haricot commun Ethiopien, initialement conduit juste sur la base de la caractérisation moléculaire, nous avions pu améliorer notrecompréhension de l'organisation de cette diversité. Nos résultats suggèrent une hybridation extensive entre les pools de gènes Andins et Mésoaméricains après une introduction du germplasm du haricot commun de l'Ethiopie.

Mots Clés: Analyse canonique discriminante, analyse en composantes principales, analyses multivariées, diversité intra-spécifique, ressources génétiques, sélection des plantes

INTRODUCTION

Two major geographic centres of domestication have endowed common bean (*Phaseolus vulgaris* L) with relatively high diversity that is broadly classified into two gene pools, Mesoamerican and Andean (Gepts and Bliss, 1986; Singh *et al.*, 1991a, b). Ever since its introduction into Ethiopia from the Americas, farmers have developed farming practices adapted to local conditions by preservation and exploitation of useful alleles, which have resulted in a range of morphologically diverse landraces (Purseglove, 1968; Westphal 1974; Wortmann *et al.*, 1998; Sperling, 2001). Moreover, efforts of the national bean-breeding programme in Ethiopia, since the 1980s, targeted towards improving on-farm productivity, have resulted in the continuous introduction of new germplasm from different parts of the world (CIAT, 2009). The existence of both gene pools (Andean and Mesoamerican) in Africa has been documented (Gepts and Bliss 1988; Asfaw *et al.*, 2009).

East Africa is often considered as a secondary centre of diversity for common bean, owing to the wide range of landraces on the continent (Allen and Edje, 1990; Wortmann *et al.*, 1998; Sperling, 2001; Asfaw *et al.*, 2009).

Ethiopia is among the major bean producers in Sub-Saharan Africa (Asfaw *et al.*, 2009). However, national average bean yield (1485 kg ha^{-1}; Cochrane and Bekele 2018) is still lagging behind those in the U.S.A. (2013 kg ha^{-1}) or in Europe (2471 kg ha^{-1}; 2016 data from FAOSTAT). This can be attributed largely to low-yielding capacity of cultivars under use, biotic/abiotic stresses, a narrow genetic base of commercial cultivars, and low soil fertility (Assefa, 1990; Fisseha, 2015). Thus, it is essential to tap the potential of landrace genetic resources in order to introgress novel genes for adaptation, resistance, and tolerance, into well-adapted elite bean cultivars.

Implications of the division of domesticated common bean into the Andean and Mesoamerican gene pools have been observed in important research and breeding areas, like

disease resistance (Burle *et al.*, 2011). Morphological characteristics, ecological distribution, and types of phaseolin/allozyme in domesticated common bean genotypes were proposed as a basis for further classification of each major gene pool into three ecogeographic races (Singh *et al.*, 1991a; Burle *et al.*, 2011). Nonetheless, no systematic study has so far been done towards identifying the ecogeographic races present among Ethiopian common bean germplasm. Asfaw *et al.* (2009) studied the genetic diversity and population structure of Ethiopian/Kenyan common bean, including a hundred of Ethiopian common bean accessions. Eventually, they reported the existence of both Andean and Mesoamerican gene pool genotypes in Ethiopia. In addition, they noted the dominance of genotypes from the Mesoamerican gene pool in Ethiopia. Even though this work has had a pivotal role towards uncovering patterns in genetic diversity and population structure of common bean germplasm from the two countries, it did not discern the identity of the groups it identified at the optimum structure cluster preset into the known ecogeographic races in both gene pools. It did not differentiate the representation of accessions from major bean-growing areas in Ethiopia.

Burle *et al.* (2011) argued that the use of morphological/agronomic characterisation of germplasm accessions provides an important biological perspective that complements a genetic characterisation, based solely on molecular markers. Furthermore, they noted that neutral genetic variation, usually assessed with molecular markers, is not always correlated with adaptive genetic variation. There is still no comprehensive information on the organisation of *P. vulgaris* diversity in Ethiopia, which integrates morphological, agronomic, and genotypic evaluations.

In a preceding study (Fisseha *et al.*, 2016), we assessed the genetic diversity and structure of collection of common bean germplasm from diverse geographic areas in Ethiopia, through application of molecular markers. Overall, this study indicated that the assessed genotypes were 24% Andean, 18% Mesoamerican, and 58% represented introgressions between the gene pools, which supported the widespread introgression between the two gene pools, which was reported previously (Asfaw *et al.*, 2009; Blair *et al.*, 2010; Angioi *et al.,* 2011). Moreover, we also identified two and three subgroups in the Mesoamerican and Andean gene pools, respectively. Consequently, it became important to identify clearly the relationships between these subgroups with the well-established domesticated ecogeographic races of common bean (Singh *et al.*, 1991a).

The objective of the present study was to integrate morphological and agronomic evaluations with the molecular diversity assessment of common bean germplasm collections obtained previously (Fisseha *et al.,* 2016). Specifically, we sought to determine to which extent subpopulations identified at the molecular level could also be distinguished at the morphological and agronomic levels.

MATERIALS AND METHODS

Sampling landrace accessions. Common bean landraces used in the study were obtained from the Gene Bank of the Ethiopian Biodiversity Institute (EBI). Six standard varieties obtained from the National Common Bean Research Project were included. Selection of accessions used was done based on the importance of the regions in terms of size of bean production, from the provided passport data. Thus, 121 landrace accessions were included in the study. Details about the collection sites and names/ numbers of accession are presented in Table 1 and Figure 1 of Fisseha *et al.* (2016). Released varieties 'Awash-1' and 'Melka Dima' were used as Mesoamerican and Andean control genotypes, respectively. The assignments of the two control genotypes was performed based on pedigree data and results of the population structure analyses using SSR markers in a

TABLE 1. States, ranges, and means for some morphological descriptors of common bean (*Phaseolus vulgaris* L.) in the groups of accessions (sub-populations)

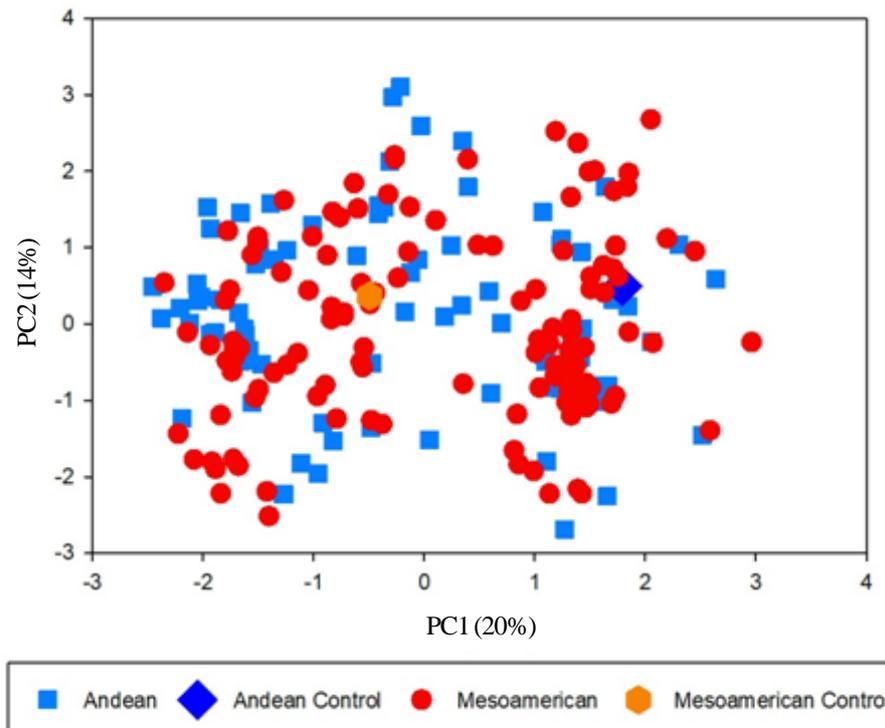| Sub-populations	Seed colour	Growth habit	Days to flowering (50%)	Standard colour	Seed Shape	Seed weight	Seed brilliance	Colour of freshly-opened flowers
K1 (A) N=5	White Cream Red	II I	51.5-56 days 54.5 days	White Dark Lilac White with red	Round (80%) Oval Kidney stripes	29.5-49.5g 37.8g	Shiny Medium	White Purple White with carmine stripes
K2 (MA) N=16	White (53%) Red Cream Brown Dull/Black	II (60%) I IV	52.5-58 days 55	White (73%) Dark Lilac White with lilac edges	Round (47%) Oval Cuboid Kidney-shaped Markedly-truncate	15.25-24.25g 19.96g	Shiny	White (67%) White with carmine stripes Purple
K3 (M) N=7	Red White Cream	II (72%) I V	51-56 days 54.25 days	White White with lilac edges Dark lilac	Oval (85.7%) Cuboid	18.5-27 g 21.36 g	Shiny Others	White White with carmine stripes Purple
K4 (A) N=11	White (55%) Red Cream	II (64%) I IV V	52-58 days 55.19	White (67%) Dark Lilac	Cuboid (36%) Oval (36%) Round	25-44.5g 36.23	Shiny (64%) Medium Others	White (91%) Purple
K5 (A) N=14	White (64%) Red Cream	II (64%) I IV	51-60.5 days 54.86	White (85%) Dark lilac	Cuboid Round Oval	24.5-62.5g 34.75g	Shiny	White Purple White with carmine stripes

Figure 1. First two principal components of diversity (PC1 and PC2) for 12 morphological variables in common bean (*Phaseolus vulgaris* L.) with respect to the Mesoamerican and Andean control gene pool genotypes.

preceding study, where membership coefficients of both were at least 99% in the Mesoamerican and Andean clusters, respectively.

Morphological evaluation. The 121 accessions of the study were grown in a field experiment at the Melkassa Agricultural Research Center (Adama, Ethiopia), during the main rainy season of 2013 (i.e., June-November). Experimental management was done according to the usual cultivation practices for common bean in the semi-arid areas of Ethiopia. The morphological descriptors were evaluated according to IBPGR (1982), with some modifications in a single replicate, according to Singh *et al.* (1991b, c). In addition, data were also collected on the following agronomic traits: seed colour, use category (i.e., dry bean vs. fresh, green pod), plant growth habit, plant

height, number of branches per plant, days to flowering, colour of flower standards, colour of flower wings in freshly-opened flowers, number of pods per plant, pod colour, number of seeds per pod, seed shape, 100-seed weight, seed brilliance, seed length, seed height, seed diameter, number of seeds per plant, and plot yield. The experimental design was simple lattice (11 X 11), with two replicates. Each plot consisted of four rows spaced 60 cm, and plants spaced 15 cm apart within rows. The two outermost rows were used as border rows, to minimise associated effects of neighbouring plots.

Genetic grouping based on molecular markers. The study samples were classified into genetic groups (two, i.e., Andean versus Mesoamerican; three, four and five groups) obtained based on the molecular characterisation of the accessions with 17

microsatellite markers, as described by Fisseha *et al.* (2016).

Data analyses. All statistical analyses were performed using R software program version 3.1.1statistical programming (R Core Team, 2014): principal component, cluster, and canonical discriminant analysis. A standardised correlation matrix and cluster analysis were used to conduct Principal Component Analysis. The Euclidean distance method was used for calculating distances, while hierarchical clustering was performed using Ward's algorithm.

A Stepwise Discriminant Analysis was first carried out to identify the morphological and agronomic variables that discriminate the two major gene pools (Andean and Mesoamerican) using the R-software programme version 3.1.1 described above. Subsequently, the variables selected in this stepwise procedure were used in a canonical discriminant analysis that was also performed according to the R statistical programming (R Core Team, 2014). To determine if the populations or subpopulations identified with molecular analysis and STRUCTURE modeling (Fisseha *et al.*,2016), also showed distinguishing morphological traits, tables with character states and ranges for some of the morphological descriptors in each group are presented for two (K = 2) and five (K = 5) groups as defined in Fisseha *et al.* (2016). The morphological descriptors presented in these tables are important descriptors for the classification of common bean races (Singh *et al.*, 1991a, b, c; Burle *et al.*, 2011). In addition, stepwise and canonical discriminant analyses were also performed with the morphological data. Seventy-two accessions were not allocated in any of the five groups when the STRUCTURE model was run at K = 5 on marker data (posterior membership coefficient below a threshold of 80%); those accessions were classified as potential hybrids (Fisseha *et al.*, 2016). Because of their presumed hybrid nature, these potential hybrids were not included in the analysis to facilitate recognition of potential

morphological differences distinguishing the different groups.

RESULTS

Principal component analysis of variation for morphological traits. Figure 1 shows the first two principal components of diversity for morphological variables in common bean [accessions were labeled according to the groups (or populations) identified by STRUCTURE software simulations with preset K = 2, i.e., Andean vs. Mesoamerican]. There was no clear separation between the Andean and Mesoamerican gene pools along these principal components (PC1: 20%; PC2: 14% of total variation). This observation contrasts with the Principal Coordinate Analysis of SSR diversity of the same materials in which there was a clearer separation between these two gene pools (Fisseha *et al.*, 2016).

Regarding the overall morphological diversity present between the two gene pools, the Andean group had equal to nearly higher diversity than that of their Mesoamerican counterparts (Fig. 1). The variation in PC1 was mostly due to significant variations in seed colour, plant growth habit, seed shape, and brilliance. On the other hand, days to flowering, colour of standard, 100-seed weight, and colour of flower-wings brought about the largest portion of the variation explained in PC1.Considering the PCA eigenvalues along PC1, most genotypes to the left of the axis had climbing growth habits, whereas non-climbing genotypes with short internodes were located to the right of this axis. The accessions with positive scores for the second principal component (PC2: 14% of total variation) were later flowering with various flower/seed colours/flower wings (in freshly opened flowers), and larger seed weight.

Morphological (and agronomic) characteristics distinguishing the Andean and Mesoamerican gene pools. A stepwise discriminant analysis was conducted involving the following 14 variables for a model that

discriminated the Andean and Mesoamerican groups, listed in the order of their entrance into the model: seed colour, plant growth habit, days to flowering, colour of flower (standard), seed shape, 100-seed weight, seed colour, seed brilliance, mean seed diameter, number of pods per plant, plant height, number of branches per plant, pod colour, and flower colour (in freshly-opened flowers). Canonical correlations corresponding to the first two axes for the canonical discriminant analysis to differentiate the two major gene pools were significantly different from zero (r = 0.98 and r = 0.68, P < 0.001).

Figure 2 shows the results of the canonical correlation analysis performed with the aforementioned variables. The results confirm those of the Principal Component Analysis in that they show extensive overlap between the Andean and Mesoamerican groups, in contrast

with the molecular classification, which provided a stronger contrast between these two gene pools (Fisseha *et al.*, 2016). The variables with larger effects on the first canonical variable (89%) were, in descending order: days to flowering, seed shape, seed brilliance, 100-seed weight, seed colour, and plant height. On the other hand, the following variables had larger effects on the second canonical variable: seed shape, seed brilliance, plant height, seed colour, 100-seed weight, and days to flowering.

Five groups based on molecular, morphological, and ecogeographic information. Canonical discriminant analysis performed with morphological data on accessions identified in K=5 of the STRUCTURE analysis in the molecular studies (Fisseha *et al.*, 2016) identified combinations
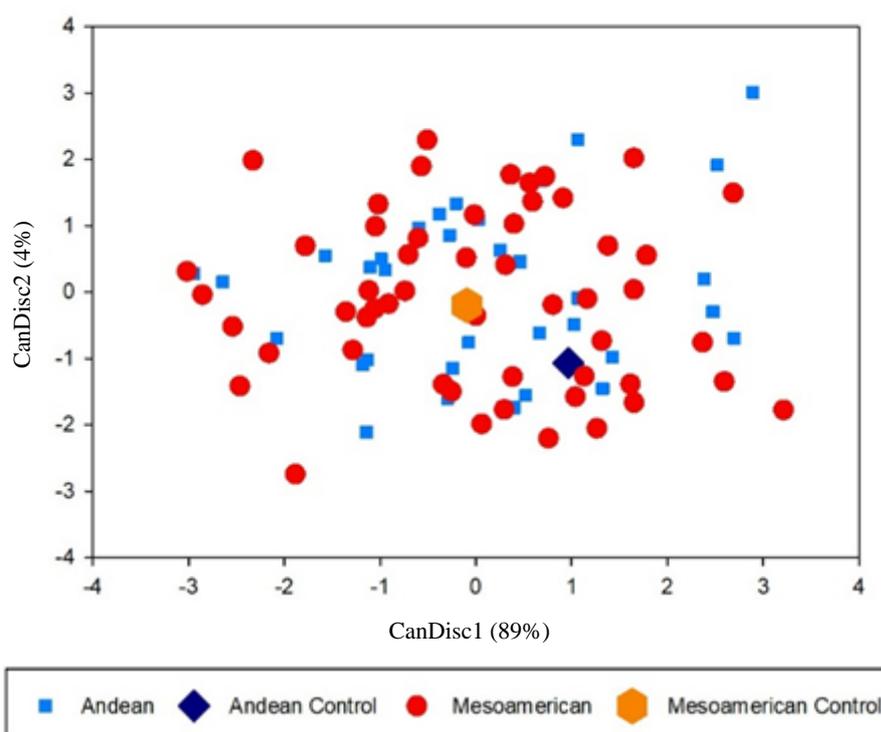

Figure 2. First two canonical variables from the canonical discriminant analysis (CanDisc1 and CanDisc2) for morphological traits discriminating Andean (blue dots) and Mesoamerican (red dots) gene pools of common bean (*Phaseolus vulgaris* L.) in the Ethiopian collection. Gene pools were identified in Fisseha *et al.* (2016) on the basis of molecular analysis (17 markers; STRUCTURE preset to K = 2).

of agro-morphological traits that were able to discriminate these five groups of accessions, three Andean and two Mesoamerican subgroups.

Where possible, the identities of the different subgroups identified by STRUCTURE were further clarified with morphological traits, which are characteristic of ecogeographic races (Singh *et al.,* 1991a; Burle *et al.* 2011). In view of this, the following interpretations as to the racial identity of each sub group were also made:

Subgroup K1 (Fig. 3: dark blue squares; N = 5) was an Andean cluster, which included the Andean control variety 'Melka Dima'. This group consisted of medium- to large-seeded accessions having various seed shapes (round, oval, and kidney) and colours (white, cream, and red) (Table 1). Accessions had Type-II (indeterminate bush) or Type-I (determinate bush) plant types, or alternatively Type-IV (indeterminate climbing) growth habit. Flowers were white, purple, and white with carmine stripes, whereas standard petals were mainly

white and dark lilac (Table 1). Predominantly, accessions in the group had round (80%) seeds, with the rest having oval and kidney-shaped seeds (Table 1).

Subgroup K2 was a Mesoamerican (MA) group (Fig. 3: orange circles; N = 16) comprising of accessions characterised predominantly by white seeds, and some red, cream or black seed colours. The majority of them were type-II (indeterminate bush) plant types (60%), though Type-I (determinate bush) and Type-IV (indeterminate climbing) also occurred with low frequencies. Seeds in this group were of small to medium sizes (<25 and 25-40 g, respectively). Seeds assumed various shapes (round, oval, cuboid, kidney, and truncated); flower standards were white, dark lilac, and white with lilac edges. Finally, flower colours (in freshly opened flowers) were white, purple, and white with carmine stripes (Table 1).

Subgroup K3 was another MA group and included the Mesoamerican control variety 'Awash-1' (Fig. 3: red circles; N = 7). It
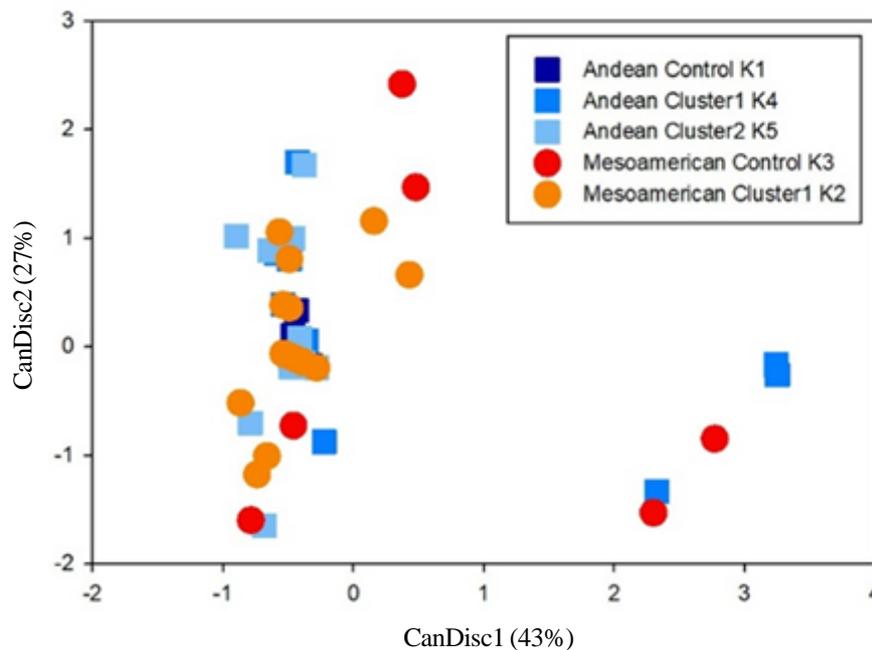

Figure 3. First two canonical variables for the canonical discriminant analysis (CanDisc1 and CanDisc2) for the five Mesoamerican/Andean groups identified based on molecular data by presetting Structure to K = 5 and without potential hybrids (Fisseha *et al.*, 2016).

consisted of seven accessions with Type-II (indeterminate bush, predominantly), Type-I (determinate bush), and Type-IV (determinate climbing) growth habits. Seeds were red, white, and cream with smaller weights (average of 21 g/100 seeds). Oval (predominantly) and cuboid were the variants of seed shapes in the group. Meanwhile, flower standards were white, with lilac edges, and dark lilac in colour, whereas flower wing petals were white and purple (Table 1).

Group K4 (Fig. 3: teal squares; N = 11) was an Andean group with accessions predominantly of Type-II (indeterminate bush) growth habit, though some Type-I and IV plant types did also occur. Seeds had medium size (mean 100-seed weight = 36 g), commonly with cuboid, oval, and round shapes. The accessions had white, red, and cream seeds, whilst having white and dark lilac flower standards (Table 1).

The final group of accessions, K5 (Fig. 3: light blue squares; N = 14), was an Andean group having medium-to large-sized seeds (25-63 g 100 seeds^{-1}) with white, red, or cream colours. Type-II (indeterminate bush) accessions predominated, with the rest having Type-I (determinate bush) and Type-IV (indeterminate climbing) growth habits. Flowers had white, white with carmine stripes, and purple colours, whereas white (predominantly) and purple were the prevalent standard colours (Table 1).

DISCUSSION

Contrast in gene pool separation between molecular and agro-morphological analyses. Our study yielded new insights into the nature of the eco-geographic racial genetic structure of the Ethiopian common bean landrace germplasm. Firstly, the analysis of agro-morphological parameters using PCA did not partition the genetic variability among accessions into the Mesoamerican and Andean gene pools in contrast with earlier data obtained solely with molecular analyses of SSR diversity. The latter analysis provided a

separation of the two gene pools, with limited overlap (Fisseha *et al.*, 2016). In our studies, neither the first axis of PCA nor that of the Canonical Discriminant analyses separated the accessions into the Mesoamerican and Andean gene pools, in contrast with previous studies in common bean (e.g., Sing *et al.*, 1991b, c; Asfaw *et al.*, 2009; Burle *et al.*, 2011). Furthermore, the intermediate positioning of many accessions, combining characters from the two gene pools of origin, as evidenced by our study, has already been documented previously (Asfaw *et al.*, 2009; Blair *et al.*, 2010).

We suggest here that this contrast between molecular and phenotypic data is due to significant introgression between the Andean and Mesoamerican gene pools in Ethiopia, such that specific traits are now found in both gene pools in the country. Evidence for the inter-gene-pool introgression is provided by the STRUCTURE analysis conducted by Fisseha *et al.* (2016), which identified 72 accessions with posterior probabilities of membership in the Andean or Mesoamerican gene pools below 0.80 for each group. Overall, our observations are consistent with previous proposals that the East African highlands, including Ethiopia, are one of the secondary centers of diversity for common bean (Westphal, 1974; Asfaw *et al.*, 2009; Blair *et al.*, 2010; Okii *et al.*, 2014a, b). They contrast with results from Brazil, another country in which the two main domesticated gene pools of common bean are present, but where introgression between these two gene pools is limited (Burle *et al.*, 2011). It also contrasts with the common bean genetic composition in other African countries, with the exception of Uganda (Table 2). In these countries, the predominant gene pool is the Andean gene pool. The important export sector of small white beans may predispose cultivation of smaller-seeded beans, which are generally of Mesoamerican origin.

Eco-geographic race representation in Ethiopian common-bean germplasm. With regard to the classification into ecogeographic

TABLE 2. Proportion of Mesoamerican and Andean genotypes of common bean reported in some African countries

Studied country	Reported proportions (%) of			Cited article
	Andean	Mesoamerican	Hybrids[1]	
Ethiopia	24	18	58	Fisseha *et al.* (2016)
Ethiopia	28	71	1	Asfaw *et al.* (2009)
Kenya	73	27	ND	
Uganda	51	49	NA	Okii *et al.* (2014a)
Tanzania	84	16	NA	Chilagane *et al.* (2016)
Malawi	85	15	NA	Guzmán e*t al.* (1995)

[1] NA = not analysed; ND = not detected

races, two races were mainly identified, namely races Mesoamerica (Mesoamerican gene pool) and Nueva Granada (Andean). Nevertheless, hybridisation among races may have blurred the limits of individual races. Burle *et al.* (2011) made a similar remark about race classification made for the sample of Brazilian common bean accessions they studied. Some of the climbing (Type IV) materials from the Andean gene pool in groups 1, 4, and 5 could also belong to race Peru. This race is usually not represented outside the Andean center of domestication because of photoperiod sensitivity with potential temperature interactions (Zeven, 1997); however, proximity of the Ethiopian highlands to the equator may have allowed introduction and survival of these Type IV materials.

Consequently, the germplasm of common bean landrace accessions in Ethiopia has a broad base in terms of diversity from the Andean gene pool (which contained two of the eco-geographic races in the Andean gene pool: 'Nueva Granada' and 'Peru'). On the other hand, it has a relatively narrow genetic base in terms of the Mesoamerican gene pool, which only belonged to the race 'Mesoamerica'. Asfaw *et al.* (2009) arrived at a similar conclusion with their study, with respect to the higher level of differentiation they observed in the Andean genotypes compared to Mesoamerican accessions. Nonetheless, their results were different from

the ones in this study in that most of their Ethiopian common bean accessions were from the Mesoamerican gene pool (Table 2). In the present study, non-hybrid Mesoamerican accessions comprised only 18% of the total accession population studied (Fisseha *et al.*, 2016). Furthermore, we have discovered the presence of only one of the three races of the Mesoamerican gene pool, i.e., race 'Mesoamerica'. The differences in the results may be attributed to the possible difference in representation of major bean growing areas in Ethiopia, and the fact that integration of morphological/agronomic data with molecular marker information had not been employed by Asfaw *et al.* (2009).

CONCLUSION

By integrating the morphological and agronomic evaluation in the diversity assessment of an Ethiopian germplasm collection of common bean, initially performed just based on molecular characterisation, we have been able to improve our understanding of the organisation of this diversity. The integration of these different kinds of data into this assessment has also allowed the identification of important differences for agronomic traits among genetic groups. Our results emphasize the importance of such an integrated approach in the diversity assessment, as a clue to promote the use of

genetic resources of large germplasm collections.

REFERENCES

Allen, D.J. and Edje, O.T. 1990. Common bean in Africa farming system. In: Progress in improvement of common bean in Eastern and Southern Africa. Smithson, J.B. (Ed.). *CIAT Africa Workshop Series* 20:32-33.

Angioi, S.A., Rau, D., Nanni, L., Bellucci, E., Papa, R. and Attene, G. 2011. The genetic make-up of the European landraces of the common bean. *Plant Genetic Resources* 9: 197-201. http://dx.doi.org/10.1017/S1479262111000190

Asfaw, A., Blair, M.W. and Almekinders, C. 2009. Genetic diversity and population structure of common bean (*Phaseolus vulgaris* L.) landraces from the East African highlands. *Theoretical and Applied Genetics* 120:1–12. http://dx.doi.org/10.1007/s00122-009-1154-7

Assefa, H. 1990. Research highlights on haricot bean in Ethiopia: an assessment of the progress, priorities, and strategies. In: *Proceedings of National Workshop*, 1-3 October 1990, Addis Ababa, Ethiopia. pp. 50-53.

Blair, M.W., Gonzalez, L.F., Kimani, P.M. and Butare, L. 2010. Genetic diversity, inter-gene pool introgression and nutritional quality of common beans (*Phaseolus vulgaris* L.) from Central Africa. *Theoretical and Applied Genetics* 121:237–248. http://www.ncbi.nlm.nih.gov/pmc/articles/PMC2886139/

Burle, M.L., Fonseca, J.R., Peloso, M., Melo, L., Temple, S.R. and Gepts, P. 2011. Integrating phenotypic evaluations with a molecular diversity assessment of a Brazilian collection of common bean landraces. *Crop Science* 51:2668–2680. https://www.crops.org/publications/cs/abstracts/51/6/2668

Chilagane, L.A., Nchimbi-Msolla, S., Kusolwa, P.M,, Porch, T.G., Serrato Diaz, L.M. and Tryphone, G.M. 2016. Characterization of the common bean host and *Pseudocercospora griseola*, the causative agent of angular leaf spot disease in Tanzania. *African Journal of Plant Science* 10: 238-245 doi: 10.5897/AJPS2016.1427

CIAT. 2009. *Bean program, annual report*. pp. 55-62, 78-85. Cali, Colombia.

Cochrane L, Bekele YW (2018) Average crop yield (2001-2017) in Ethiopia: trends at national, regional and zonal levels. Data in Brief 16: 1025-1033

Durán, L.A., Blair, M.W., Giraldo, M.C., Macchiavelli, R., Prophete, E., Nin, J.C. and Beaver, J.S. 2005. Morphological and molecular characterization of common bean landraces and cultivars from the Caribbean. *Crop Science* 45: 1320-1328. https://dl.sciencesocieties.org/publications/cs/abstracts/45/4/1320

Fisseha, Z. 2015. Genetic diversity and population structure of common bean (*Phaseolus vulgaris* L.) from Ethiopia. Ph.D. Thesis, Addis Ababa University, Addis Ababa, Ethiopia. 221 pp.

Fisseha, Z., Tesfaye, K., Dagne, K., Blair, M., Harvey, J., Kiallo, M. and Gepts, P. 2016. Genetic diversity and population structure of common bean *(Phaseolus vulgaris* L)

germplasm of Ethiopia as revealed by microsatellite markers. *African Journal of Biotechnology* 15:2824-2847. http://www.academicjournals.org/journal/AJB/article-full-text/528FF4562176

Gepts, P. and Bliss, F.A. 1986. Phaseolin variability among wild and cultivated common beans (*Phaseolus vulgaris*) from Colombia. *Economic Botany* 40:469–478.

Gepts, P.and Bliss, F.A. 1988. Dissemination pathways of common bean (*Phaseolus vulgaris*, Fabaceae) deduced from phaseolin electrophoretic variability. II. Europe and Africa. *Economic Botany* 42:86-104.

IBPGR. 1982. Phaseolus vulgaris *descriptors*. IBPGR, Rome, Italy.

Martin, G.B. and Adams, M.W. 1987. Landraces of *Phaseolus vulgaris* (Fabaceae) in northern Malawi. I. Generation and maintenance of variability. *Economic Botany* 41:204-215.

Okii, D., Tukamuhabwa, P., Kami, J., Namayanja, A., Paparu, P., Ugen, M. and Gepts, P. 2014a. The genetic diversity and population structure of common bean (*Phaseolus vulgaris* L.) germplasm in Uganda. *African Journal of Biotechnology* 29:2935-2949. http://www.academicjournals.org/journal/AJB/article-abstract/59E971146091

Okii, D., Tukamuhabwa, P., Namayanja, A., Mukabaranga, J., Paparu, P. and Gepts, P. 2014b. Morphological diversity of tropical common bean germplasm. *African Crop Science Journal* 22:59-67. http://www.ajol.info/index.php/acsj/article/view/101372

Purseglove, J.W. 1968. *Tropical crops: dicotyledons*. Wiley, New York, USA.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Singh, S.P., Nodari, R. and Gepts, P. 1991a. Genetic diversity in cultivated common bean. I. Allozymes. *Crop Science* 31:19-23. https://dl.sciencesocieties.org/publications/cs/abstracts/31/1/CS0310010019

Singh, S.P., Gutiérrez, J.A., Molina, A., Urrea, C. and Gepts, P. 1991b. Genetic diversity in cultivated common bean: II. Marker-based analysis of morphological and agronomic traits. *Crop Science* 31:23-29. https://dl.sciencesocieties.org/publications/cs/abstracts/31/1/CS0310010023

Singh, S.P., Gepts, P. and Debouck, D.G. 1991c. Races of common bean (*Phaseolus vulgaris* L., Fabaceae). *Economic Botany* 45:379–396.

Sperling, L. 2001. The effect of the civil war on Rwanda's bean seed systems and unusual bean diversity. *Biodiversity Conservation* 10:989-1009. https://link.springer.com/article/10.1023%2FA%3A1016628310917

Westphal, E. 1974. Pulses in Ethiopia, their taxonomy and agricultural significance. Pudoc, Wageningen, the Netherlands.

Wortmann, C.S., Kirkby, R.A., Eledu, C.A. and Allen, D.J. 1998. Atlas of common bean (*Phaseolus vulgaris* L.) production in Africa. CIAT Pan-African Bean Research Alliance, vol 133.

Zeven, A.C. 1997. The introduction of the common bean (*Phaseolus vulgaris* L.) into Western Europe and the phenotypic variation of dry beans collected in The Netherlands in 1946. *Euphytica* 94:319-328. http://dx.doi.org/10.1023/A:1002940220241