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Cover illustration:
Work on the bean collection of the CIAT gene bank in Colombia (Neil Palmer, CIAT) as featured in the Review "History and impact of a bean (*Phaseolus* spp., Leguminosae, Phaseoleae) collection" by Debouck et al, pp. 21-43.

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'Zeitoun Ennour': A new olive (*Olea europaea* L.) cultivar in Tunisia with high oil quality

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Abstract: An olive breeding program was started in Tunisia in 1993 in order mainly to improve the fatty acid composition of the local cultivar 'Chemlali Sfax'. 'Zeitoun Ennour' is a new cultivar obtained from a cross between 'Chemlali Sfax' and the local dual-purpose use cultivar 'Chemchali Gafsa'. The morphological study of this cultivar showed that eleven characters dealing with fruit and endocarp differed from 'Chemlali Sfax', mainly regarding to their respective weights. This new cultivar had the same sensitivity to *Verticillium dahliae*Kleb and earlier bearing than the original variety. Its olive production was considered as high as for 'Chemlali Sfax' but with partial self-compatibility and late maturity. The new cultivar realized a net improvement in comparison with the original cultivar particularly regarding its fatty acid composition with very high oleic acid content (>75 %) and low palmitic and linoleic acid contents (<10 %). The new cultivar was recently released and will be available for growers as soon as possible.

Keywords: Chemlali Sfax, new cultivar, morphology, fatty acids, agronomy

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Introduction

Attempts to develop new olive cultivars have been carried out in many olive-producing countries (Italy, Turkey, Israel, Spain, Tunisia, Egypt, Iran, China, Ukraine and Turkmenistan) as reported by Bellini *et al* (2008). Most of these programs have focused on cross-breeding among the most outstanding cultivars in their respective countries.

In Tunisia, a breeding program has been carried out within the context of the project 'olive breeding' (supported by the International Olive Council) since 1994. In this program, the cultivar 'Chemlali Sfax' was crossed with both autochthonous and foreign olive varieties as pollen donors, yielding 1,200 seedlings. The goal of this program was to improve the acidic composition the oil, since 'Chemlali Sfax' has low oleic acid (55%) and high palmitic acid (19.6%) (Zarrouk *et al*, 2009; Bellini *et al*, 2008).

Several studies have shown the dietary importance of fatty acid composition of lipids. A healthy diet should contain a limited amount of saturated fatty acid (e.g. palmitic acid) to reduce the total cholesterol content and a high amount of monounsaturated fatty acid (e.g. oleic acid) which was shown to prevent the risk of cardiovascular diseases, reduce the insulin body-requirement and decrease the plasma concentration of glucose (D'imperio *et al*, 2007). According to Zarrouk *et al* (2009), monounsaturated fatty acids have great

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importance because of their nutritional implication and effect on the oxidative stability of oils. According to Barranco *et al* (2000), the low content of oleic acid for the 'Chemlali Sfax' olive cultivar is considered as a deficiency that should be resolved. High oleic acid content is also a breeding objective in sunflower (Neto *et al*, 2016) and peanut (Godoy *et al*, 2014). For example, breeding efforts in peanut have led to the release of two genotypes with much higher concentration of oleic acid (Godoy *et al*, 2014).

Many studies were undertaken on seedlings of the 'Chemlali Sfax' breeding program regarding morphological description (Laaribi *et al*, 2014; Guellaoui *et al*, 2019) and acidic composition of the oil (Manaï *et al*, 2007; Rjiba *et al*, 2009; Dabbou *et al*, 2010; Ben-Amar *et al*, 2019). Morphological characteristics of the 'Chemlali Sfax' olive tree seedlings showed a high genetic variability. Also, these studies revealed high variability in the main fatty acid concentrations and several seedlings had a chemical composition more interesting than that of the original cultivar.

Recently, five new cultivars obtained in the Tunisian crossbreeding program were released and published in the Official Journal of Republic of Tunisia (JORT, 2017). Two released hybrids were already reported by Guellaoui *et al* (2019) and Ben-Amar *et al* (2019). According to these authors, the two new cultivars (Zeitoun Ennwader and Chemlali Mhassen) were mainly characterized by better fatty acid composition regarding to oleic and palmitic acid contents than the original cultivar 'Chemlali Sfax'.

Regarding abiotic stresses, Elloumi *et al* (2016) studied the tolerance of several hybrids to salinity stress in comparison with the original cultivar 'Chemlali Sfax'.

The objective of this study was to describe the main morphological, agronomic and oil quality characters of another released olive cultivar 'Zeitoun Ennour' in comparison with the original cultivar 'Chemlali Sfax'.

Material and methods

Plant material

'Zeitoun Ennour' is a new olive (*Olea europaea* L.) cultivar obtained in a crossbreeding program in Tunisia. It was derived from a cross carried out in 1993/1994 between 'Chemlali Sfax' (female) and 'Chemchali Gafsa' (male), two cultivars from different geographical origins: 'Chemlali Sfax' from Sfax in the center-wast of Tunisia and 'Chamchali Gafsa' from Gafsa in the center-west of Tunisia. 'Chemchali Gafsa' showed better fatty acid composition when compared to 'Chemlali Sfax', the most widely adopted olive cultivar in Tunisia as reported by Grati-Kamoun and Khlif (2001).

The cross was performed by pollination of flowers on bagged branches with fresh pollen grain and forced growth of seedlings was carried out in a greenhouse to shorten the juvenile period. Seedlings were planted in two open fields during 1997-1998 with a density of 1250 trees/ha (4 x 2m spacing): the experimental station of the Olive Institute at Sfax (Central Tunisia, lat 34° 44′ N, long 10° 46′ E) and the Research Station of 'Taous', which is about 26 km from Sfax (lat 34° 56′ N, long 10° 36′ E).

The first crop was obtained in 2000 and seedling evaluation was carried out for three consecutive harvest seasons. The original seedling of 'Zeitoun Ennour' was selected mainly on the basis of its fatty acid composition. After vegetative propagation by semi-hardwood stem cuttings (2002 to 2004), propagated trees of 'Zeitoun Ennour' together with other selected seedlings were planted in a comparative trial since 2005 at 6 × 4m spacing and irrigated conditions at the experimental farm of 'Taous' in the region of Sfax.

Methodology

The evaluation of 'Zeitoun Ennour' and the check 'Chemlali Sfax' in this trial was done for three trees per cultivar during three years (2013-2015) on the following characters:

Morphology

Morphological description was carried out each year according to the procedure of IOC (International Olive Council, 1997a) by using a total of 21 characters recorded on 40 leaves (2 characters), 40 fruits (10 characters) and their endocarps (9 characters). One sample was taken from the productive trees each year. Leaves and fruits were harvested together when the fruit skin was almost yellow-purple and leaves were collected from the middle part of one-year old shoots.

Agronomy

Agronomic characters were recorded according to the IOC norms (International Olive Council, 1997b). Bearing earliness was determined as the number of years of the first significant bearing after planting in 2005. This number was recorded for each cultivar when more than 50% of the plants were already in production. Olive production was evaluated on the same three trees during the three years. The olive production per tree was usually recorded in November.

The ripening index was determined according to the formula of Hermoso *et al* (1991) based on the colour of the skin and the pulp and varied between 0 and 7. This index was determined on a sample of 100 fruits collected every week from November to January from the productive trees and the date which corresponded to the optimal index for harvest equal to 3.5 (International Olive Council, 1997b) was recorded.

Pollen compatibility was determined by choosing two floral branches for each tree and recording fruit sets obtained from cross-pollination (not bagged branch) and self-pollination (bagged branch). According to Barranco *et al* (2000) , a cultivar is considered self-compatible when the two fruit set values are similar, partially self-compatible when fruit set from self-pollination is less than that from cross-pollination and self-incompatible when fruit set from self-pollination is zero.

The tolerance test to *Verticillium dahliae* Kleb was undertaken in greenhouse conditions on five one year old plants per cultivar. The inoculation was made by wetting the plants in a conidial suspension adjusted to 10^6 conidia/ml. Cultivars were classified into five categories according to their AUDPC average (Area Under Disease Progress Curve) established previously by Lopez-Escudero *et al* (2004): highly resistant (HR), 0 to 10 %; resistant (R), 11 to 30 %; moderately susceptible (MS), 31 to 50 %; susceptible (S), 51 to 70 %; and extremely susceptible (E), 71 to 100 %.

Fatty acid composition

Each year, representative olive samples were harvested from the productive trees when the maturity index was approximately 3.5 (optimum maturity). Olive oil was produced by grinding 2.5 kg stoned olives and extracting the oil by mechanical means, following standard methods used in oil factories, including milling and malaxation. The fatty acid composition of the oils was determined by gas chromatography (GC) as fatty acid methyl esters, using a Hewlett-Packard model 4890D gas chromatograph. Fatty acids were identified by comparing their retention times with those of standard compounds. Three major fatty acids were evaluated in this study, palmitic acid (C16:0), oleic acid (C18:1) and linoleic acid (C18:2) and their concentrations in 'Zeitoun Ennour' were compared with those of the original cultivar 'Chemlali Sfax'.

Data analysis

For each morphological character, the type having the highest mean value over three years was attributed to the cultivar. Bearing earliness can be very early (< 3 years), early (3 years), medium (4 years), late (5 years) or very late (> 5 years). The ripening date corresponding to maturity index 3.5 can be in late autumn (early maturity), early winter (medium maturity) or late winter (late maturity).

Variance analysis was made for olive production and Verticillium tolerance considering years and plants as replicates respectively. For pollen compatibility, variance analysis was undertaken for each cultivar to compare fruit sets from self-pollination and free pollination considering years as replicates. For oil chemical characters, variance analysis with years as replicates was carried out for each fatty acid.

All data analyses were performed using the statistical procedures in XLSTAT 11.0 and the separation of means was done by Duncan test at 5 % level.

Results and discussion

Morphological characterization

The morphological evaluation of the new cultivar is presented in Table 1 and Figure 1. Leaves of 'Zeitoun Ennour' were mostly of elliptic-lanceolate shape and flat longitudinal curvature similar to the original cultivar.

Figure 1. Leaf, fruit and endocarp of 'Zeitoun Ennour' olive cultivar. Scale in cm.

Fruits of the new cultivar were asymmetrical, with a truncated base and rounded apex, medium weight, central maximum diameter, few lenticels, and without nipple. At maturity stage, the location of colour change start was uniformly across the whole epidermis and the colour at the end of maturity was black.

'Zeitoun Ennour' had asymmetric endocarp with medium weight, elliptic shape, a round base, pointed apex, its maximum diameter toward the apex, rugose surface and regular distribution of grooves. The apex termination was without mucro.

This cultivar differed from the typical of 'Chemlali Sfax' in more than half of the scored fruit and endocarp traits, (11 traits in total), especially regarding their respective weights, where 'Zeitoun Ennour' scored higher (> 2 g and > 0.3 g respectively) than 'Chemlali Sfax' according to IOC norms (International Olive Council, 1997a). Chemlali Sfax was previously shown to have low fruit and endocarp weights (Barranco *et al*, 2000; Trigui and Msallem, 2002).

Despite the evidence of the subjectivity of the morphological description, it can be concluded that the new cultivar showed substantial genetic differences from 'Chemlali Sfax'. Laaribi *et al* (2014) reported wide genetic diversity observed within and between olive tree seedlings issued from the same Tunisian breeding program.

Agronomic characterization

An agronomic description of 'Zeitoun Ennour' and 'Chemlali Sfax' was carried out a the comparative field trial established at the experimental farm 'Taous' of the Olive Tree Institute (Table 2).

The new cultivar showed a short juvenility period (3 years) from planting till economic bearing. It can be classified with early bearing in comparison with 'Chemlali Sfax' (medium). Yield traits were evaluated on 10-year-old trees during the period 2013-2015, the average yield per tree was classified as high for both cultivars similar what had previously been reported for 'Chemlali Sfax' (Barranco *et al*, 2000; Trigui and Msallem, 2002).

Table 1. Description of the main morphological characters of olive cultivar ‘Zeitoun Ennour’ compared with the control ‘Chemlali Sfax’. PDM : Position of Maximum transverse Diameter

Organ	Character	Zeitoun Ennour	Chemlali Sfax
Leaf	Shape	Elliptic-Lanceolate	Elliptic-Lanceolate
	Longitudinal curvature	Flat	Flat
Fruit	Weight	Medium	Low
	Shape	Ovoid	Ovoid
	Symmetry	Asymmetric	Symmetric
	PDM	Central	Central
	Apex	Rounded	Rounded
	Base	Truncate	Truncate
	Nipple	Absent	Absent
	Start of colour change	Uniform	Apex
	Lenticels	Many	Few
	Maturity colour	Black	Black
Endocarp	Weight	Medium	Low
	Shape	Elliptic	Elliptic
	Symmetry	Asymmetric	Symmetric
	PDM	Toward apex	Central
	Apex	Pointed	Rounded
	Base	Rounded	Pointed
	Surface	Rugose	Smooth
	Distribution of groves	Regular	Regular
	Apex termination	Without mucro	With mucro

‘Zeitoun Ennour’ displayed late maturity with optimum ripening period occurring in late winter while ‘Chemlali Sfax’ displayed medium maturity.

Regarding pollination mode, fruit set following self-pollination (5.13 %) was significantly inferior to that following crosspollination (9.87 %). Consequently, the new cultivar was found to be partially self-incompatible according to the norms of Barranco *et al* (2000). ‘Chemlali Sfax’ had a self-compatible behavior in our study since fruit sets from self-pollination and cross-pollination were statistically similar (11.21 and 10.45 % respectively). The same performance was reported for ‘Chemlali Sfax’ by Trigui and Msallem (2002) in the centre of origin. Thus, while pollinator trees may not strictly be required in the field with this new cultivar, several pollinator trees planted in the orchards could compensate for the partial self-incompatibility, as suggested by Mehri *et al* (2003) in these situations. In this case, a study of the flowering period for different olive varieties is necessary to identify the best pollen donor for ‘Zeitoun Ennour’.

With respect to *Verticillium dahliae* Kleb, our results indicated that ‘Zeitoun Ennour’ and ‘Chemlali Sfax’ had similar levels of tolerance with 65 and 57 % respectively. Consequently, they were susceptible to this fungus. Thus, we suggest propagating this new cultivar with semi hardwood cuttings from healthy trees in order to avoid *Verticillium* infection. Morever, the best solution in the propagation of this cultivar is to follow the plant certification procedure as outlined in the EU plant health regulation (European Commission, 2016) to ensure the *Verticillium* free status of olive plants. In fact, *Verticillium* wilt is the most destructive disease affecting olive orchards in Tunisia (Gharbi *et al*, 2020) and in the world (López-Escudero and Mercado-Blanco, 2011).

Fatty acid composition

The ‘Zeitoun Ennour’ cultivar had a considerably improved fatty acid composition compared to the original cultivar ‘Chemlali Sfax’ (Table 3).

Table 2. Description of the main agronomic characteristics of the new olive cultivar compared with ‘Chemlali Sfax’. Means for each character followed by the same letter are not significantly different except for fruit set where the comparison was made between self-pollination and cross-pollination for each cultivar.

Character	Zeitoun Ennour	Chemlali Sfax
Earliness of bearing	3^b	4^a
Olive production per tree (kg)	12.2^a	10.5^a
Ripening	Late winter (Late)	Early winter (medium)
Fruit set (self-pollination) (%)	5.13^b	11.21^a
Fruit set (cross-pollination) (%)	9.87^a	10.45^a
Verticillium tolerance (%)	65^a	57^a

Table 3. Mean fatty acid concentrations (%) of the new cultivar 'Zeitoun Ennour' compared with 'Chemlali Sfax' and corresponding IOC norms (International Olive Council, 1997b). For each fatty acid, different letters following the means indicate significant differences at 5 % level

Character	Zeitoun Ennour	Chemlali Sfax	IOC norm
Oleic acid	76.3^a	59^b	55 – 83
Palmitic acid	10.0^a	19.6^b	7.5 – 20
Linoleic acid	9.7^a	16.8^b	2.5 – 21

In comparison with the original variety, the mean values of 'Zeitoun Ennour' for the three fatty acids were significantly better than the original variety. The concentration of oleic acid, the main monounsaturated fatty acid, was higher for the new cultivar (76.3 %) than the original cultivar (59 %), while the level of palmitic acid, the major saturated fatty acid in olive oil, was significantly lower (10 %) than 'Chemlali Sfax' (19.6 %). The content of linoleic acid, another important monounsaturated acid, for 'Zeitoun Ennour' was also lower (9.7 %) than 'Chemlali Sfax' (16.8 %).

In addition, the fatty acid composition of 'Zeitoun Ennour' is within the standard norms reported by the International Olive Council (1997b), while 'Chemlali Sfax' practically has the lowest value of oleic acid and the maximum limit of palmitic acid.

According to D'imperio *et al* (2007) and Zarrouk *et al* (2009), a healthy olive oil should have high oleic acid content and low palmitic acid content. Thus, we consider that the new selected cultivar 'Zeitoun Ennour' realized an important genetic gain in fatty acid composition and could be of great benefit in the Tunisian olive sector (farmers, industrials and oil exporters). From the same breeding program, two other hybrids were released and characterized. Zeitoun Ennwader (Chemlali Sfax/Lucques) and Chemlali Mhassen (Chemlali Sfax autopollinated) were presented, respectively, by Ben-Amar *et al* (2019) and Guellaoui *et al* (2019).

Conclusion

'Zeitoun Ennour' was registered by the Tunisian Ministry of Agriculture, Hydraulic resources and Fisheries (MARHP) under number 191 in January 2017 (JORT, 2017). The propagation of this new cultivar will be assured as soon as possible through a certification procedure. Simultaneously, this new cultivar is under evaluation in rain fed conditions in Tunisia.

The crossbreeding program in Tunisia since 1993 has allowed selection of superior olive genotypes which could increase the economic input of the oil sector.

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Author contributions

Imen Guellaoui performed all the measurements and notations, Fathi Ben Amar and Olfa Elloumi wrote the manuscript and processed the experimental data, Mohamed Ali Triki executed fungi tests, Mohamed Ayadi performed oil quality tests and Mohsen Boubaker supervised the work. All authors read and approved the final manuscript.

Conflict of interest statement

The authors declare no conflict of interest.

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Local breeds and pastoral farming on the North Mediterranean shore: a univocal coevolution? An example of dairy sheep farming systems in Corsica (France) and Thessaly (Greece)

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Abstract: Using local resources for ruminant feeding is a way to achieve agroecological production in pastoral farming systems. In North Mediterranean countries, sheep farming systems have evolved towards more intensive systems in lowland and hilly areas, whereas remote and rough pastureland is abandoned and local breeds are rarely maintained; rather, they are progressively replaced by highly productive breeds and their crosses. Using the examples of Corsica (France) and Thessaly (Greece), two dairy sheep farming territories developing intensive farming systems that differ in the livestock breeds they use, we explored the hypothesis that the use of local breeds may not be systematically related to the maintenance of pastoral practices in Mediterranean dairy sheep farming systems. For this purpose, three data sets based on interviews with sheep farmers of local breeds and crossbred flocks were analysed in two study areas. The results demonstrated that local breeds' adaptive abilities can be used in crossbred flocks or purebred flocks to maintain a feeding system based on pastoral components. However, other drivers also appear to lead into the declining use of local pastoral resources. Apart from the use of local breeds, year-to-year adjustments of replacement and culling rates sometimes have to be applied in order to address the inter-annual variations of the fodder on offer. This paper provides an original approach to studying the link between local breeds and the pastoral components of farming systems by combining synchronic and diachronic analyses of the practices in crossbred and purebred flocks composed of local breeds.

Keywords: Crossbreeding, grazing, breeding practices, Karagouniko sheep breed, Corsican sheep breed

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Introduction

The agroecological transition in livestock farming relies on decreasing farm inputs and increasing the use of local feed resources and farm leftovers to meet the needs of the on-farm production procedure and on grazing modalities closely following ecological processes in order to ensure the renewal of resources in the long term (Jouven *et al*, 2010; Dumont *et al*, 2013). Worldwide, in pastoral farming systems of dairy sheep and other ruminant species, feed requirements are

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covered to a varying degree through grazing of local fodder resources under a range of management systems (FAO, 2001). Grazing on a diversity of fodder plant species on rangelands also aids the conservation of landscapes (D'Ottavio *et al*, 2016) and limits soil erosion resulting from continuous cropping (Schnabel *et al*, 2009) in a way that is not competing with the use of land for other food production. Moreover, grazing of local resources promotes the biological interactions between animals and their biophysical environment, providing an interesting basis to design agroecological production systems (Dumont *et al*, 2013).

Despite these benefits, pastoral farming systems are disappearing, mostly in disadvantaged areas, but also in favourable sites of North Mediterranean countries, leading to degradation of traditional rural landscapes (Hadjigeorgiou *et al*, 2005; Caballero *et al*, 2009). The disappearance of pastoral activity in many regions in recent decades has revealed the importance of sustainable livestock management for environmental conservation. The absence of pastoralism has had negative consequences on biodiversity and ecosystem services, particularly in marginal areas traditionally used for this activity (Constanza *et al*, 1997). In many ecosystems with a deep-rooted grazing tradition, such as those of the Mediterranean (Hadjigeorgiou, 2011), the withdrawal of livestock farming activities has led to broad negative changes in the richness and diversity of plant species (Sternberg *et al*, 2000). Moreover, the abandonment of pastoral farming has led to modification of various interspecies interactions, affecting negatively, for instance, pollinators, herbivorous insects, parasitoids and birds (Plieninger *et al*, 2006; Dover *et al*, 2011). Similarly, this change favoured woody vegetation encroachment, leading to the accumulation of fuel biomass and consequently raising the danger of wildfires (Rosa-García *et al*, 2012). At the same time, ruminants' farming systems have evolved towards intensive ones and established in more accessible areas, such as lowlands and hilly areas of the mainland. Examples include reports on zero grazing in Castilla-Leon in Spain or sedentary intensive or semi-intensive systems in Greece (Caja and de Rancourt, 2002; de Rancourt *et al*, 2009), the abandonment of winter transhumance under agricultural pressure in the Ebro valley in Spain (Caballero *et al*, 2009) or the replacement of permanent grasslands by agriculturally improved pastures in Italy (Porqueddu *et al*, 2017).

In parallel, the evolution of flock composition in breeds and their crosses shows different patterns in Mediterranean regions subjected to intensification of farming systems and decreased use of native grazing resources. For example, in north and central Spain, as well as in Greece, farms with highly productive sheep breeds and their crosses coexist with those of local sheep breeds[1] (e.g. (de-la Fuente *et al*, 2006; Perucho *et al*, 2018). However, in other North Mediterranean regions, also subjected to intensification of farming systems, local breeds remain the main genetic resources in sheep farming. In the South of France, for instance, the Black-Face Manech and the Red-Face Manech are traditionally raised due to their hardiness in the transhumant systems of the West Pyrenees, although the Red-Face Manech now prevails over the Black-Face Manech in most intensive farming systems of the area (Labatut, 2009; Lauvie *et al*, 2015). Likewise, in the Crau region in France the Merino breed is used due to its specific transhumance ability, but it is also raised in many different sedentary farming systems, including mixed farming systems with an intensive use of land, based on cereals and hay cropping (Moulin *et al*, 2004; Lauvie *et al*, 2015). Moreover, holdings with local sheep breeds are found in many different biogeographical regions in Italy under sedentary or itinerant systems often combined with cropping (Caballero *et al*, 2009).

We thus hypothesized that the use of local breeds may not systematically ensure the preservation of pastoral practices in Mediterranean dairy sheep farming systems. In order to test this hypothesis, we explored holdings using different livestock breeds, as well as the evolution of their feeding systems with emphasis on pastoral practices. In particular, we focused on two production territories where dairy sheep farming systems were based on the use of different livestock breeds or their crosses, while they were subjected to similar trends towards intensification. Each case study brought up features from different situations to illustrate our argumentation.

Material and methods

Choice of the study areas and specific objectives

Holdings with different livestock breeds considered in the study were those with a) local sheep breeds traditionally raised in pastoral systems, b) highly productive breeds (either exotic or native, raised in more intensive farming systems) and c) crosses of these breeds. The evolution of pastoral practices was analysed through two approaches, (i) a direct one: mid-term analysis of changes in feeding systems (changes in grazing lands and supplementation), and (ii) an indirect one: a study of the diversity of feeding systems found in a territory at any one time and their past trajectories of intensification. The choice of the approach depended on the genetic resources considered. The two study areas chosen to cover this diversity of situations towards livestock breeds and feeding systems were the regions of Thessaly (central Greece) and Corsica (South of France).

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[1] Local breeds are defined in this paper as breeds linked to a specific territory (e.g. Georgoudis *et al*, 2001; Loukovitis *et al*, 2016; Perucho, 2018)

The outputs of these two case studies hereinafter are successively presented in the results section.

Thessaly is a region of central Greece composed of two central plains occupying half of the land area and bordered by mountainous chains that are traditional transhumance regions (Sivignon, 1975). The lowland part of Thessaly is characterized by a continental climate with cold winters, hot summers, and wide annual temperature ranges, while in the mountainous part summer temperatures are cooler. Typical grazing areas both in lowlands and highlands are composed of both grasslands and shrublands. In the last few decades, the region's holdings were subjected to an intensification trend centred on harvested feeds, encouraged by a combination of various subsidies, a favourable economic context (low price for feeds compared to the price of milk) or by the proximity of crops for animal consumption in the lowlands (Perucho *et al*, 2015). In this context, highly productive breeds with high feed requirements were progressively adopted since the 1970s. Nowadays, the breeds used by sheep farmers are multiple and include the three above mentioned categories, ranging from local breeds under recording schemes (e.g., the Karagouniko breed) or conservation programmes (e.g., the Kalarritiko breed) and other local animal populations, to highly productive breeds raised in purebred or crossbred flocks. Several changes in the genetic composition of the flocks were taking place at the time of the study. The objective of data collection in this region was (i) to understand the farmers' reasoning for choosing the specific breeds composing current flocks, and to identify among them the reasons linked to the feeding system in place (data set T1), and (ii) to compare recent changes of flock genetic composition and changes of feeding systems and identify possible causal relations (data set T2).

Corsica is an island in the South of France structured around two central mountainous ranges bordered by a narrow plain on the eastern side of the island. Below an altitude of 1200 m (all sampled farms were located below this altitude), the typical rangeland vegetation is composed of shrublands and woodlands and the climate is Mediterranean with a marked summer drought period and irregular rainfalls with local variations due to microclimates and altitudinal gradients (Gamisans, 1999). Sheep farming in Corsica is considered as pastoral, but has evolved since the 1960s towards an increasing use of cultivated grasslands and supplementation levels, and a decrease of transhumance (Santucci, 2010; Choisis and Vallerand, 1992). *N*owadays, in spite of this intensification process, the Corsican sheep breed, traditionally raised in pastoral farming systems, is almost exclusively used in the region. Dairy sheep farming thus relies on purebred Corsican breed flocks, of which approximately 15% were included in the ewe breeding scheme of the Corsican breed in 2015. The objective of the data collection in this region was to investigate the different feeding systems in which this local breed is currently raised and identify possible differences in the pastoral components of these feeding systems. Additional information on breeding practices (culling and replacement rates) was collected at the same time in order to identify whether the feeding system could impact, if not on the reared breed, at least on its management through culling and replacement.

Data collection

The three data sets that were considered in the study to respond to the above mentioned specific objectives are presented in Table 1. Data were collected between October 2014 and May 2016 (dataset T1) and in 2016-2017 (dataset T2 and C1) through semi-structured interviews with farmers.

The sampling method for both case studies covered a diversity of feeding systems and focused on different sheep breeds. Information on regional feeding systems and their geographical distribution was obtained from the existing literature for Corsica (Paoli *et al* (2014) and Thessaly (Goussios *et al*, 2014; Perucho *et al*, 2015). In samples of C1 and T1 datasets, for purebred flocks of local breeds, attention was paid to address both flocks participating in the breeding scheme and flocks not participating in the breeding scheme. For dataset T2, interviews were focused on the changes from local breeds to their crosses with highly productive breeds and thus concerned flocks whose composition has evolved from local breed populations towards crossbred animals.

The interviews performed included close-ended and open-ended questions. Farmers' responses could have different levels of detail depending on the respondent, but in all cases, interviews gave specific attention to the collection of comprehensive information on on-farm practices (Kaufmann, 2011). The interviews were held face-to-face, while clarifications and additional information were subsequently obtained through telephone interviews, when needed.

Data collected and considered in the study are presented in Table 1. In interviews C1, the management of replacement and culling rates was considered under routine situations and perturbations, including the inter-annual variations of fodder on offer. In interviews T1, the selection of breeds composing the flocks and the crossbreeding strategy were explained by the farmers through their reasoning for choosing or rejecting each breed with respect to its characteristics. Interviews T2 were conducted on the basis of the conceptual framework of the analysis of the changes in livestock farming systems (Moulin *et al*, 2008), and they aimed to identify non-varying objects and sequences of transformations or progressive modifications to the components of the farming activity. For this purpose, farmers informed the interviewer about the year they began to change the initial genetic composition of their flock, mostly through performing crossbreeding with highly productive breeds. Data were collected for the year preceding the first introduction of a new breed in the flock and for the years during which a change occurred in these components, along with the

Table 1. Characteristics of data collected in this study

Study area	Thessaly		Corsica
ID data set	T1	T2	C1
Data collection mode	Semi-structured interviews with farmers		
Number of farms	N=42	N=14	N=30
Targeted sample	Diversity of flock genetic compositions - Diversity of feeding systems	Crossbred flocks with highly productive breeds (previously local breeds) - Diversity of feeding systems	Purebred flocks of Corsican breed ewe - Diversity of feeding systems
Data collected and considered in the study	Agricultural land composition, Grazing and feeding management, Flock composition, Breeds and crossbreeding strategy	Changes in: Supplementation diet, Grazing management, Surface and use of land, Breeds involved in the flock genetic composition	Agricultural land composition, Grazing and feeding management, Flock composition, Replacement and culling

reasons motivating the change. All relevant changes were recorded until the year of the study.

Definition of the pastoral components

A range of definitions of pastoral systems can be found in the literature (Tchakerian, 2008; FAO, 2001). These definitions are mainly based on the presence or absence of the following components: a) seasonal movements of grazing animals, b) nature of grazing areas, c) proportion of the diet relying on native vegetation and d) knowledge and know-how related to grazing practices. In this paper, the term pastoral components" is used to describe the modalities of use of spontaneous vegetation (characteristics of grazing areas) and its relative importance in the feeding systems. More information on the variables considered is provided in the following section.

Data analysis

Thessaly

Data collected in Thessaly were analysed in two steps.

In the first step, using data set T2, the chronology of changes in feeding systems (supplementation levels and composition, importance of grazing and natural pastures, area for cropping animal feeds) and flock genetic composition (breeds introduced in the flock or abandoned), were described. The pastoral components of the feeding systems were defined according to the following modalities: low supplementation levels and high level of use of natural pastures. We analysed the evolution of these pastoral components by comparing the variations of supplementation levels, as well as the variations, in the use of natural pastures and crops for animal feeds over time. We either compared two values at different time points or used qualitative data on the evolution of the variables over time, (represented by triangles in Figure 1). Then, possible causal relations between changes in the feeding system and change in flock genetic composition were identified and addressed as follows: (i) defining the level of adaptation of the new genetic composition of the flock to the existing feeding system, as observed by the farmer, then (ii) detailing the different responses of the farmers to offset any failure in adaptation (see results).

Then, among the range of farmers' responses (T2), we focused on the reintroduction of breeding animals from local rustic breeds (Karagouniko breed), in order to reinstate the flock's adaptation to the existing feeding system. Among the reasons for choosing local rustic breeds, specific characteristics related to the hardiness of the breed and associated constraints of the feeding system were listed. This reasoning was compared to outputs of interviews T1 on the reasons for introducing or rejecting different breeds in the flock (see also Table 4). The effect of such reintroduction was discussed by considering the evolution of the feeding system after the reintroduction of a local breed (T2).

Corsica

In Corsica, farming systems were characterised in terms of the feeding system and the breeding practices (replacement and culling). The related descriptors are presented in Table 2. Among the five descriptors of the feeding system presented in Table 2, the variables used to describe pastoral components were, a) the percentage of flock's energy requirements covered through grazing at the annual level, b) the part of cultivated grasslands in the total agricultural area of the holding and c) the nature of the grazing areas. The percentage of the flock's annual energy requirements covered through grazing was derived from the total energy requirements minus the percentage covered by supplementary feed (roughage and concentrates) using feed tables (INRA, 2007). Descriptors of breeding practices (replacement rate in routine situations and under variations of fodder offer, see Table 2) expressed the strategies implemented by the farmers to secure the necessary fodder for their flocks, under inter-annual climate fluctuations.

In order to compare farms according to these two categories of variables, the different modalities were represented for each farm, on coloured and grey-scale matrix (Bertin, 1983). This representation allowed the differentiation of farms, with flocks of Corsican sheep breed, into a range of feeding systems and the identification of specific breeding practices (aimed to

Table 2. Variables built for the analysis of the data derived from the C1 interviews, subsequently used for Bertin's graphical representations

Category of variable	Variable	Variable code
Feeding system (results in Figure 2)	Role of grazing in covering total flock energy requirements	ROLE GRAZING
	Self-sufficiency in hay production	HAY PRODUCTION
	Share of cultivated grasslands to the total agricultural land	CULTIVATED GRASSLANDS
	Location of the farm	LOCATION
	Practice of transhumance	TRANSHUMANCE
Replacement and culling (results in Figure 3)	Routine replacement rate	REP RATE
	Influence of variation of forage availability on culling rate	FORAGE VAR/CULL RATE
	Influence of variation of forage availability on replacement rate	FORAGE VAR/REP RATE

secure fodder on offer) in groups of farms raising the same breed under different feeding systems.

Results

Comparative evolution of feeding systems and crossbreeding practices in Thessaly

Figure 1 illustrates changes in the feeding systems (in terms of supplementation, grazing and crops for animal consumption) and the breeds introduced in the flocks of 14 dairy sheep farms in Thessaly after the first crossbreeding with a highly productive breed (first yellow square of each line). Among these numerous changes of breeds and feeding systems, several were justified by farmers after a failure of the new breed to adapt to the existent feeding system. Starting from these specific cases, we analysed the different drivers of evolution of breeds and feeding systems in the short and long-term.

Introducing highly productive breeds displayed a lack of adaptation to existing feeding systems

A lack of adaptation of newly introduced, highly productive breeds (or their crosses) in the flock to existing feeding strategy and grazing conditions was mentioned by nine farmers. These inconsistencies between breeds and feeding systems took three forms: (i) the breed/crossbreed was deemed not hardy enough to function under existing grazing conditions; (ii) the feeding strategy implemented for the breed was considered economically unsustainable; and (iii) the various breeds, raised simultaneously in the flock, had different feeding requirements, but it was not practical to implement a different feeding practice for each of them (Table 3).

Three types of farmers' responses (adjustments) to this lack of adaptation were identified. The first type was the modification of the feeding/grazing strategy towards decreasing the role of native resources in the applied production system, represented by red stars in $. The second type consisted of the rejection of the highly productive breed in use and/or the testing of a new breed: farmers adopted an exploratory behaviour towards locally available breeds, leading to several changes in breeding animals in a short time period, according to availabilities offered by the market and consultation with other farmers in the region and elsewhere. The third type of farmers' response was the reintroduction of breeding animals from the local hardy Karagouniko breed in the herd, represented by brown triangles in Figure 1.

In some farms, the failure of the highly productive breeds to adapt to the feeding system in place was not explicitly mentioned by the farmer, but feeding systems were modified after their introduction. Some of these changes in feeding systems occurred in the general frame of the intensification of farm production means, i.e. the purchase of highly productive breeding animals (yellow squares in Figure 1) came with an investment in feed quantity and quality, housing, equipment and task mechanization in order to maximize the expression of the specific breed's productive potential. The introduction of a highly productive breed and the decrease of grazing and/or the change in diet quantity or quality generally occurred simultaneously or within a short time period after breed introduction (example of changes in farms 1, 2, 3, 4, 5 or 6 during the decade 2000-2010, Figure 1).

Other changes in feeding systems were driven by the following four factors: (i) a change in land access (example of farm 8 since 2003, Figure 1, (ii) economic or climatic perturbations, (iii) a modification of the role of sheep farming in the family's income and (iv) the increase in average flock size. They occurred at different moments regardless of the change of breed (examples of changes in farms 9 and 13 in 1995 and 1997-1998, respectively). The above mentioned drivers of change could be combined (one perturbation implies farm intensification). For example, in mixed farming holdings, traditionally based on cash crops and sheep farming (farms 3,5 and 6 in Figure 1), the combination of decreasing cotton prices (since the 2000's) and the decoupled subsidies for cotton crops (since 2006) led to an increasing role of sheep farming in the family income, together with the search for new alternatives to cotton crops. According to farmers' economic possibilities, subsequent changes in sheep farming activities were immediate (farms 5 and 6) or progressive (farm 3) and included the testing of different, highly productive breeds combined with high supplementation levels and

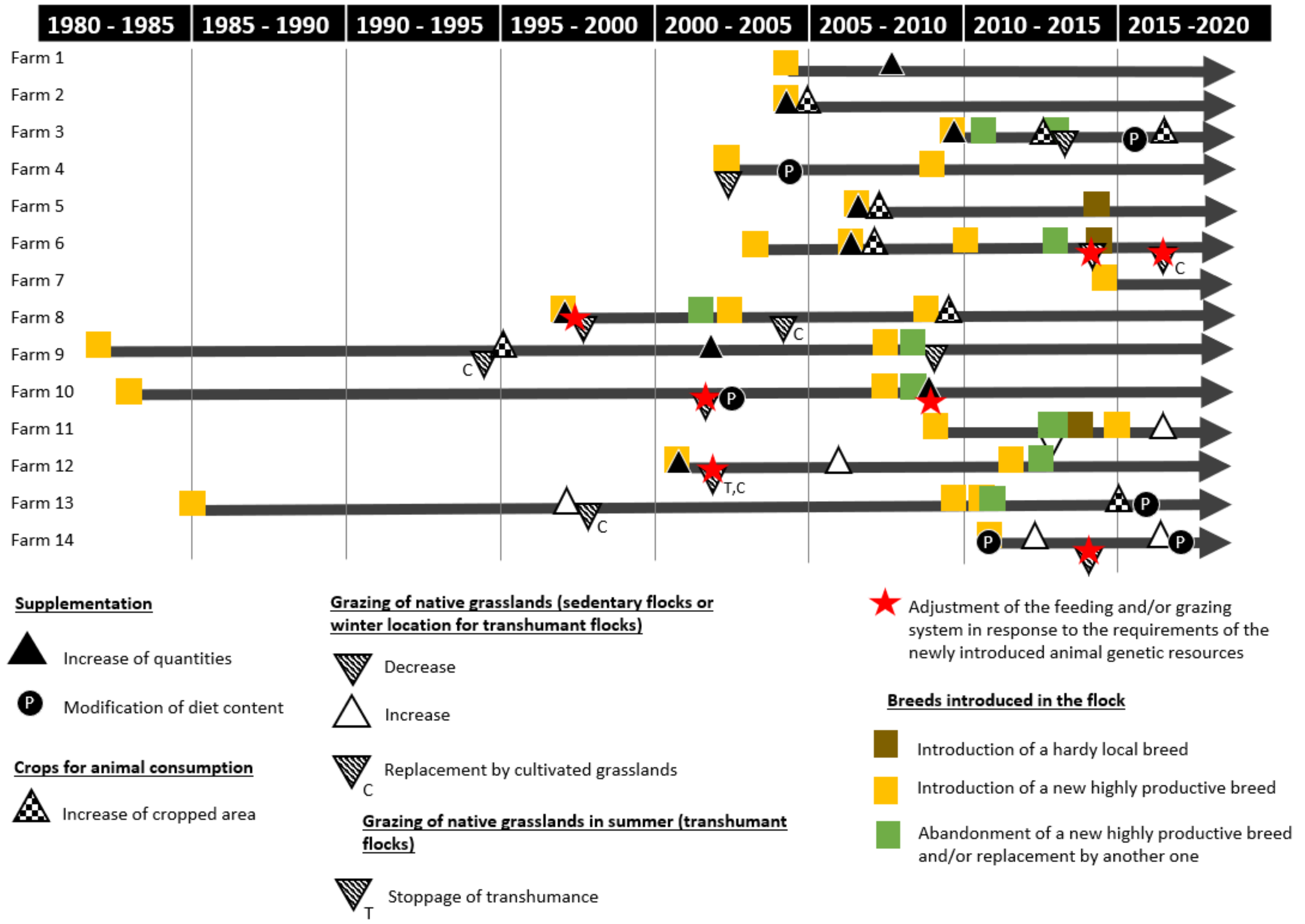


Figure 1. Comparative evolution of the flocks' breed compositions as well as the feeding and grazing systems in 14 dairy sheep farms in Thessaly, Greece.

the replacement of cotton crops by crops destined for animal feeding.

Introduction of Karagouniko local breed for hardiness was not necessarily associated with maintenance of pastoral components

The reintroduction of the local Karagouniko breed was operated by farmers in three of the nine farms for which inconsistencies between flock genetic composition and feeding system were mentioned. In farmers' statements, the characteristics of the highly productive breeds/crossbreeds forcing such changes in the flock genetic composition were the following: high sensitivity to thermic stress (n=2), high cost of feeding (n=1), high cost of animal health care or high sensitivity to mastitis (n=2), inefficient performance on pasture (n=1), a lack of adaptation to transhumance (n=1), and difficulty in hand milking (n=1). Likewise, the results from the T1 interviews indicated that the dairy sheep farmers of Thessaly utilised local breeds in their holding in order to improve the hardiness of the flock (in terms of adaptation to pastoral conditions) and rejected highly productive breeds for their incapacity to do so. These abilities and the breeds used or rejected for their corresponding characteristics are presented in Table 4.

However, in the medium and long-term, the pastoral components of the feeding systems of those three farms were not necessarily maintained. In the first farm (farm 5), maintaining grazing on communal grasslands, in order to keep feeding costs low, was part of the farmer's strategy according to his statement. Reintroduction of Karagouniko purebred animals aiming to keep a hardy flock, several years after the first crossbreeding, allowed the farmer to maintain this grazing practice for the following years (farm 5 in Figure 1). In a second farm (farm 6 in Figure 1), reintroducing the Karagouniko breed, through crossing, was motivated by the low capacity of the highly productive breeds to cope with climatic constraints. However, the newly composed crossbred flock remained disappointingly sensitive to thermal stress, as well as to health risks on communal grasslands, which led the farmer to decrease grazing a few years after the introduction of the local breed. In a third farm (farm 11 in Figure 1) using native grasslands (including summer pastures through transhumance) was part of the farmer's strategy but, ultimately, the maintenance of this practice competed with workload management. In this case, crossbreeding with the local breed temporarily delayed the stoppage of transhumance. However, the introduction of machine

Table 3. Components of the feeding system and the traits of the breed involved in the different forms of inconsistencies mentioned by farmers in Thessaly

Inconsistency (number of farms)	Component of the feeding system at stake	Traits of the breed at stake (number of mentions)
Lack of hardiness (n=8)	Grazing conditions (Climatic conditions)	Sensitivity to thermal stress (n=1)
	Grazing conditions (Duration of grazing/nature of the foraging resource)	Feeding mode leading to sensitivity to mastitis and ruminal pathologies (n=1)
	Grazing conditions (Presence of pathogens)	Sensitivity to vector-borne diseases (n=2)
	Grazing conditions (Distance and topography)	Walking ability (n=3)
Feeding costs (n=5)	Grazing conditions (Open-field pastures)	Grazing behaviour (n=2)
	Feed supply (quantities at the multiyear scale)	Longevity (n=2)
	Feed supply (quantities at the yearly scale)	Feeding requirements (n=3)
Competition between breeds (n=1)	Feed supply (quantities at the yearly scale)	Feeding intake (n=1)

milking led this farmer towards a sedentary system (this is not presented in the figure, but it was planned as a short-term project by the farmer at the year of the interview). It is also interesting to mention that the modalities of the introduction of the local breed in these three farms were limited to the introduction of breeding males in the specific year that the problem was observed and it was not followed by a concrete crossbreeding plan with the introduced local breed.

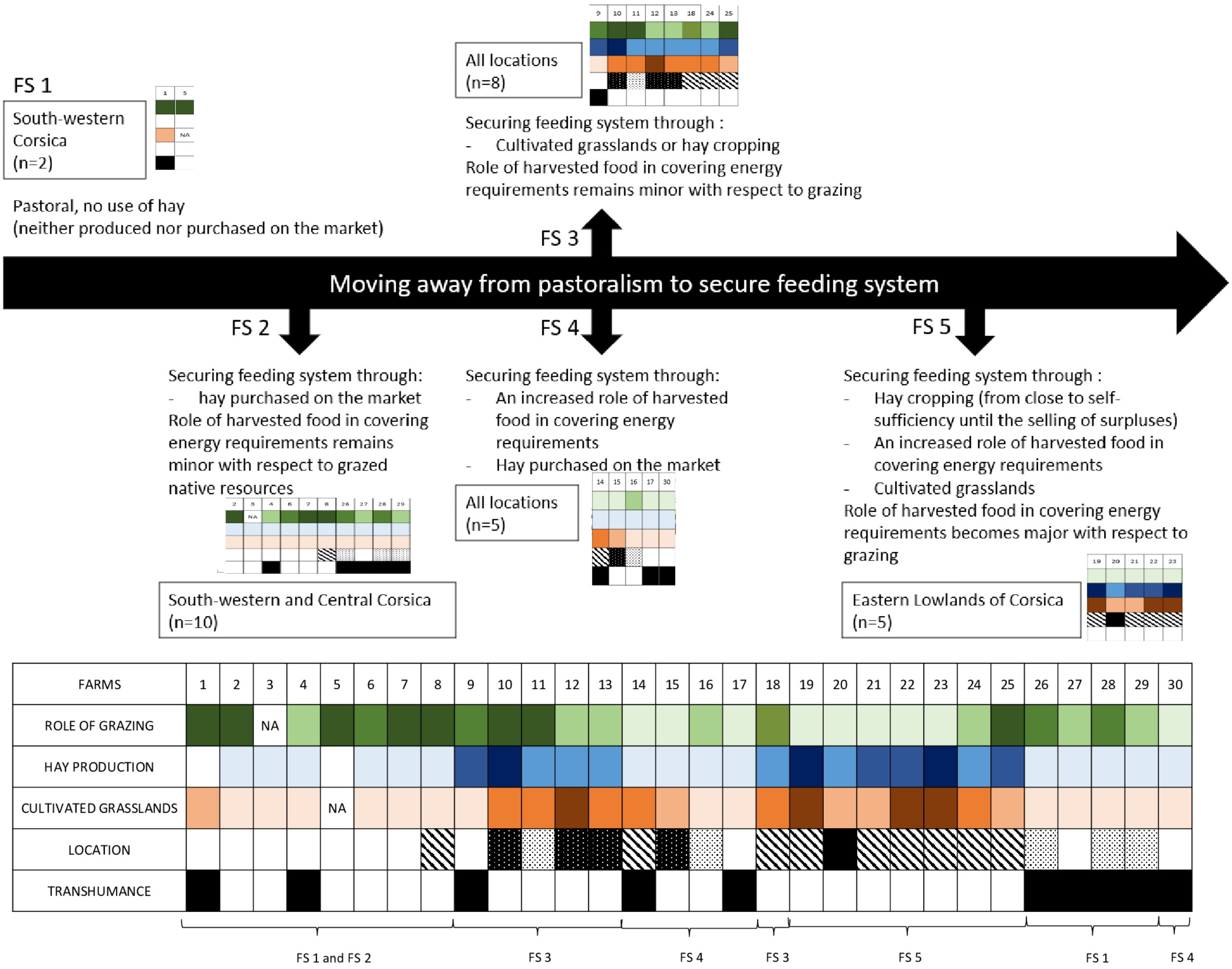
Local purebred flocks in a diversity of feeding systems in Corsica

Currently, different feeding systems can be observed among local purebred flocks of Corsica (Corsican sheep breed), ranging from the most pastoral to the most intensive in feeding inputs and land use and including both transhumant and sedentary flocks.

Figure 2 presents a classification of five types of feeding systems (FS1 to FS5) according to the role of grazing in covering the energy requirements, the type of grazed pastures and the farmers' strategy with respect to the provision of hay. Most of the pastoral systems (characterized by less harvested feed energy used compared to that of grazed native resources) are found in southwestern and central Corsica (FS1 and FS2), the most intensive feeding systems (in terms of feeding inputs and workload for fodder production) are located in the eastern coastal lowlands (FS5), and the intermediate feeding systems are found in all locations of the island (FS3 and FS4). This current situation of local breed dairy sheep farming conditions in Corsica reflects a trend towards the securing of feeding systems, either by on-farm fodder production in areas with favourable agroecological conditions, or by hay purchased at the market. The diversity of land use in Corsica, for the 206 dairy sheep farms using the Corsican breed, has also been documented by Perucho *et al* (2020)

Table 4. Breeds' traits motivating the introduction or rejection of a specific breed in the flock: the case of traits linked to pastoral farming. Hardiness (or a similar term) was used by farmers to characterize the overall ability of the breed to withstand the constraints of its raising conditions.

Reasons for introducing or rejecting a specific breed (traits linked to pastoral farming)	Percentage of sampled farmers mentioning the trait (n=42 farmers)	Breeds used (in bold) or rejected (normal font)
Ability to handle transhumance	14% (n=6)	**Kalarritiko breed**
Low sensitivity to cold and high humidity	50% (n=21)	**Karagouniko breed and local populations** Chios, Lacaune, and Frizarta/Friesian breeds
Low sensitivity to heat	45% (n=19)	**Karagouniko and Awassi breeds** Frizarta/Friesian and Assaf breeds
Hardiness	48% (n=20)	**Karagouniko, Kalarritiko, Piliou and local populations** Chios and Lacaune breeds
Behaviour compatible with grazing	26% (n=11)	**Karagouniko breed** Lacaune breed



Pastoral, no use of hay
(neither produced nor purchased on the market)

Securing feeding system through :
- Cultivated grasslands or hay cropping

Role of harvested food in covering energy requirements remains minor with respect to grazing

Securing feeding system through:
- hay purchased on the market

Role of harvested food in covering energy requirements remains minor with respect to grazed native resources

Securing feeding system through:
- An increased role of harvested food in covering energy requirements
- Hay purchased on the market

Securing feeding system through :
- Hay cropping (from close to self-sufficiency until the selling of surpluses)
- An increased role of harvested food in covering energy requirements
- Cultivated grasslands

Role of harvested food in covering energy requirements becomes major with respect to grazing

Variable		Modalities
Role of grazing in covering total flock energy requirements (ROLE GRAZING)	🟩	70% or more of yearly flock energy requirements are covered by grazing
	🟩	60% to 70% of yearly flock energy requirements are covered by grazing
	🟩	50% to 60% of yearly flock energy requirements are covered by grazing
	🟩	Less than 50% of yearly flock energy requirements are covered by grazing
	NA	No data was available (n=1)
Self-sufficiency in hay production (HAY PRODUCTION)	□	No use of hay
	🟦	All hay used is purchased on the market
	🟦	50% of self-sufficiency in hay production or self-sufficiency is very variable due to interannual climatic variations
	🟦	The majority or all the hay used is routinely produced on-farm
	🟦	All hay used is routinely produced on farm and the farmer can sell/often sell surpluses
Part of cultivated grasslands in agricultural land (CULTIVATED GRASSLANDS)	🟫	More than 25% of the agricultural land is covered by cultivated grasslands
	🟧	From 10% (included) to 25% of the agricultural land is covered by cultivated grasslands
	🟧	Less than 10% of the agricultural land is covered by cultivated grasslands
	🟧	No cultivated grasslands
	NA	No data was available (n=1)
Location of the farm (LOCATION)	░	(points fond blanc) Central Corsica
	□	(white) South-Western Corsica
	■	(black) Corsican Cap
	▓	(points fond noir) North-Western lowlands
	▨	(hachures) Eastern lowlands
Practice of transhumance (TRANSHUMANCE)	■	(black) Transhumant flock
	□	(white) Sedentary flock

Figure 2. Diversity of the feeding systems among the local purebred flocks in Corsica (results on 30 farms)

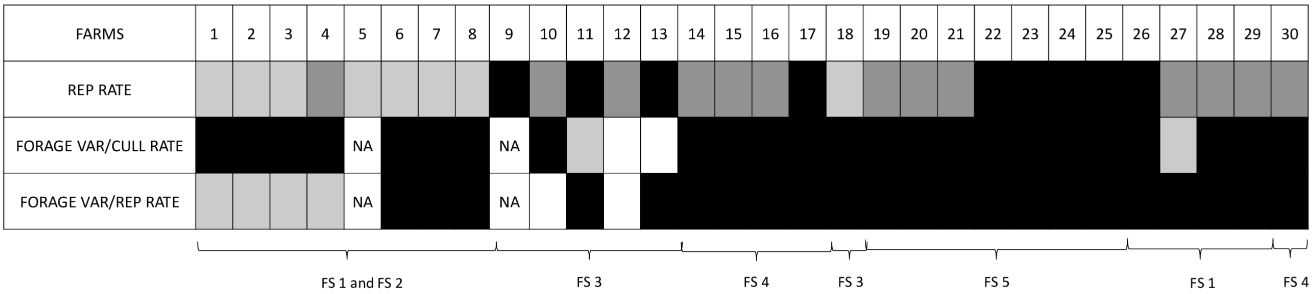
Adaptation to variations of fodder on offer through replacement and culling management in local purebred flocks of Corsica

In addition to the use of local breeds in purebred flocks, several of the interviewed farmers performed specific breeding practices in order to maintain the same feeding system in spite of the variations in climatic conditions and subsequent fodder offer. These breeding practices consisted of adjusting the demography of the flock according to inter-annual variations of fodder on offer. In some pastoral systems of southern and central Corsica (farms 1, 2, 3 and 4; included in FS1 and FS2, Figure 3, this consisted of increasing the replacement rate in years with good forage offers (FORAGE VAR/REP RATE, line 4 of the table in Figure 3) and of reversing the practice in years of low forage offers. Moreover, in pastoral systems FS1 and FS2, the observed replacement rates were generally low (less than 20%, REP RATE, see line 2 of the table in Figure 3). Another adaptation of the flock demography consisted of increasing the culling rate in order to limit the number of animals that feed during the lambing period of the following year (farms 11, 12, and 13, FORAGE VAR/CULL RATE, line 3 of the table in Figure 3). This practice was observed in farming systems relying partly on cultivated forage (FS3) in areas of the island impacted by a dry microclimate (e.g. north western lowlands), resulting in variable fodder production from one year to another. These examples, although concerning only a small number of farmers of the sample, demonstrate that the use of a local breed might be combined with other breeding practices so that the farmer is able to maintain the same feeding system from one year to another.

Discussion

Our results indicate that the practice of crossbreeding with highly productive breeds in Thessaly is often connected with the intensification of feeding by increasing the quantity of feed inputs and modifying the diet with the aim of improving its quality. Similarly, the use of local breeds is usually linked with the applied pastoral practices and prevailing climatic conditions. Boyazoglu and Hatziminaoglou (2005) described the long-term evolution of feeding systems in the European part of the Mediterranean basin, characterised by a decrease in transhumance and the use of grazing areas, while the population of small ruminants maintained its genetic composition. On the other hand, Couix *et al* (2016) showed that, in dairy cow holdings, the replacement of the Holstein breed by dual purpose local breeds in the western part of France was associated with an overall evolution of the farming systems towards decreased production costs, including the costs associated with the feeding system. In this study, a change in breed was often followed by the adoption of pasture-based feeding systems. Samdup *et al* (2010) analysed the adoption of crossbreeding with different exotic, highly productive breeds in a range of cattle farming systems in Bhutan (from extensive to intensive livestock farming systems) and the impact of crossbreeding on such farming systems four years after its implementation. They observed a lower adoption rate of crossbreeding in extensive and semi-intensive farms with the farms either keeping the local breed or rejecting one specific exotic breed (among the two introduced) due to its high feed requirements. The authors also mentioned that during lactation, crossbred cows were stall fed, resulting in reduced grazing in forest and natural grasslands in comparison to local cattle (Samdup *et al*, 2010). The same conclusions were drawn in a study in Ethiopia (Roschinsky *et al*, 2015), where most of the cattle farmers adopting crossbreeding with exotic breeds changed their grazing and feeding management towards restricted grazing and the purchase of compound feeds or household by-products, while feed shortages and feed prices were the drivers for rejecting the practice of crossbreeding. Caballero *et al* (2009) also mention the decline of some indigenous breeds in Spain, Italy and Greece and the abandonment of extensive livestock farming in marginal areas. Apart from diachronic studies, studies dealing with farmers' preferences for breeds' traits emphasize the key role of local breeds' adaptive traits in pastoral systems (Kosgey *et al*, 2008; Tamou *et al*, 2018) and the preference for exotic breeds in agropastoral systems benefitting from best pastures and climatic conditions (Konig *et al*, 2015). These results agree with the first part of our results associating, on the one hand, crossbreeding for higher productivity with feeding intensification and, on the other hand, local breeds with lower feeding inputs in pastoral systems.

However, these two associations are not systematically observed, and farmers do not necessarily abandon raising local breeds following an intensification process. The example of Corsica, where one local breed is raised under feeding systems with different levels of intensification, and the one of Thessaly, where a variety of genetic types can be found at different stages of the intensification process, suggest that additional studies are needed in order to more convincingly conclude whether coevolution of local breeds and feeding systems is regionally univocal. The data collected through interviews should be compared with the physiological and behavioural responses of highly productive sheep breeds and their crosses in pastoral farming systems in North Mediterranean countries. Methods to predict breeds' suitability to environmental conditions are proposed, in this sense, by (Lozano-Jaramillo *et al*, 2018) and (Marshall, 2014), but these concern South Mediterranean or tropical systems. In the case of North Mediterranean countries, there are fewer pastoral components and the climatic conditions are milder, but the need for adaptive potential of the animals to similar environments is increasing in importance due to intensifying climatic changes (Hoffman, 2013). In this sense, learning processes regarding grazing (Meuret and Provenza, 2014) and genetic selection should also be considered



FARMS	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
REP RATE	░	░	░	▓	░	░	░	░	■	▓	■	▓	■	▓	▓	▓	■	░	▓	▓	▓	■	■	■	■	■	▓	▓	▓	▓
FORAGE VAR/CULL RATE	■	■	■	■	NA	■	■	■	NA	■	░	□	□	■	■	■	■	■	■	■	■	■	■	■	■	■	░	■	■	■
FORAGE VAR/REP RATE	░	░	░	░	NA	■	■	■	NA	□	■	□	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■

Variable		**Modalities**
Routine replacement rate (REP RATE)	■	Routine replacement rate is 20% or more
	▓	Routine replacement rate goes from 15% (included) to 20% (excluded) or minimum replacement rate in routine is 15%
	░	Routine replacement rate is less than 15%
Influence of forage variation on culling rate (FORAGE VAR/CULL RATE)	■	Forage variations from one year to another does not influence culling rate
	░	A low forage offer can slightly increase culling rate
	□	A low forage offer frankly increases culling rate
	NA	No data was available (n=2)
Influence of forage variation on replacement rate (FORAGE VAR/REP RATE)	■	Forage variations from one year to another does not influence female replacement rate
	░	A high forage offer can slightly increase female replacement rate
	□	A high forage offer frankly increases female replacement rate
	NA	No data was available (n=2)

Figure 3. Adjustment of the flock demography according to the inter-annual variations of the fodder offers in Corsica (C1, n=30)

when assessing the suitability of North Mediterranean breed types. Finally, our results illustrate that defining the “pastoral dimension” of North Mediterranean systems implies considering a set of pastoral components assessed not in terms of absolute value, but also in relative value: pastoral components of one farm are described with regard to the other farming systems of the area. Accordingly, detailing constraints of feeding systems by pastoral components might be useful in the assessment of breed suitability.

The fact that feeding systems in an area can evolve independently from animal genetic resources used there, is not analysed per se in current research, but rather is suggested by the diversity of factors known to affect the maintenance of pastoral components and the management of animal genetic resources. The evolution of small ruminant feeding systems towards decreased pastoral components is well documented in different Mediterranean countries (de Rancourt *et al*, 2009). The drivers of this decrease, as depicted in recent literature, echo the findings of the present study: the farmers wish to alleviate the labour-consuming tasks associated with the feeding system, which leads to a decrease in grazing (Aubron *et al*, 2016). Other factors such as the farmers’ mind-set and their social environment, the absence of markets for products based on grazing, as well as land fragmentation have been shown to influence the decision to graze or not to graze in European dairy cow holdings (Dasselaar *et al*, 2020). In Greece, the economic context (in terms of prices and subsidies) favoured the choice of purchasing feed outside of the farm (Stefanakis *et al*, 2007; Volanis *et al*, 2007; Hadjigeorgiou, 2011), together with other factors such as the low quality of spontaneous forage material, the difficulty to access communal rangelands and an inadequate rangeland management system. Other examples from small ruminant farming in Greece also illustrate that the legislative framework can force the settlement of nomadic farmers through specific requirements for facilities to comply with milk and stock hygiene standards, animal welfare and manure management (Hadjigeorgiou, 2011). Finally, the trend towards agricultural intensification in easily accessible productive lands led to land use changes through abandonment of mountainous areas in southern Europe and shrub encroachment in many remote areas formerly used for grazing (MacDonald *et al*, 2000; Caballero *et al*, 2009). This phenomenon is highly dependent on EU agricultural and natural conservation policies (Tzanopoulos *et al*, 2011).

Likewise, the diversity of factors affecting the evolution of animal genetic resources in flocks has to be taken into account. According to (FAO, 2015), the reported main causes of genetic erosion in 23 countries in Europe and the Caucasus (in response to open-ended questions) mostly consisted of (i) breeds not profitable/competitive or that have poor performance (48% of the countries), (ii) intensification of production or decline of traditional production systems or small-sized farms (39% of the countries) and/or (iii) the introduction/increased use of exotic breeds (35% of the countries). Indeed, the introduction of exotic breeds through uncontrolled crossbreeding (failure or absence of crossbreeding programmes) greatly compromised the conservation of local breeds (Leroy *et al*, 2016b). More than 20% of the above mentioned countries also mention problems in breed management linked to weak or absent management policies, programmes or institutions (FAO, 2015). Indeed, except for their adaptive traits, local breeds in European countries are also kept (being the first motivation) for their links with tradition and their importance in society and, unequally among countries and breeds, for the economic incentives and conservation programmes that benefit them (Gandini *et al*, 2010). In this context, the successes or failures faced by national genetic management programmes and the associated involvement of researchers in such management (Leroy *et al*, 2016a) directly impact the evolution of local breeds' populations. In Greece, for example, the state-run genetic management of local breeds has suffered several interruptions in financing, impacting the implementation of data recording (Georgoudis and Ligda, 2000). Together with unfavourable dairy policies, the problems in the implementation of breed management programmes have been impacting on, for example, the breeding scheme of the Karagouniko breed in Thessaly (e.g. Perucho *et al,* 2019). On the other hand, the financial support, through EU-funded agri-environmental measures, aimed at farmers raising local breeds threatened by extinction, together with the support provided to farmers in mountainous or disadvantaged areas, has succeeded in maintaining local breed populations over time, as is, for example, the case for the pastoral sheep farming systems of the Kalarritiko purebred flocks (National Rural Network, 2019).

Conclusion

The example of long-term changes in dairy sheep farms in Thessaly, Greece, indicated that dairy sheep farmers sometimes use local breeds in crossbred flocks in order to improve flock hardiness after a first crossbreeding with highly productive breeds. In this strategy grazing practices can be maintained and feeding costs reduced together with other health costs. In some cases, the shift to new exotic breeds was also considered as an alternative to local breeds in order to improve flock hardiness. However, any additional factors impacted the management of feeding systems, such as local trends towards intensification, access to production means (e.g. land, workforce, capital) and workforce management. This resulted in an evolution of feeding systems (decrease of grazing on native grasslands – increase of supplementation) not necessarily in accordance with the initial reason for the introduction of the local breed in the flock (the maintenance of pastoral components of the feeding system). Likewise, although the Corsican sheep breed is considered as hardy, its use could be maintained in different feeding systems including systems engaged in an intensification process. Finally, farmers in Corsica chose to act on flock structure to adapt to several constraints linked to the forage offer in their local purebred flocks. This result indicated that the use of a local breed in purebred or crossbred flocks should be combined with several other practices or conditions so that raising local breeds remains closely related to the pastoral activity.

By demonstrating a non-univocal co-evolution between local breeds and farming systems, this study highlights the need to better characterize local and exotic breeds' abilities as well as farmers' strategies to cope with different perturbations of their environment. This knowledge will help maintain pastoral systems in production territories and the livestock breeds associated with these territories.

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Author contributions

The authors confirm contribution to the paper as follows: study conception and design: Lola Perucho, Anne Lauvie, Charles-Henri Moulin, Jean-Christophe Paoli, Christina Ligda; data collection: Lola Perucho; analysis and interpretation of results: Lola Perucho, Ioannis Hadjigeorgiou, Anne Lauvie, Charles-Henri Moulin, Jean-Christophe Paoli, Christina Ligda; draft manuscript preparation: Lola Perucho; manuscript revision: Lola Perucho, Ioannis Hadjigeorgiou, Anne Lauvie, Charles-Henri Moulin, Jean-Christophe Paoli, Christina Ligda.

Conflict of interest statement

The authors declare that no conflict of interest exists.

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History and impact of a bean (*Phaseolus* spp., Leguminosae, Phaseoleae) collection

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Abstract: This work explains the reasons why a bean collection was established in 1973 at the International Center of Tropical Agriculture (CIAT) near Palmira in Colombia. It shows the impact of the collection on plant breeding and in agricultural development through the distribution of germplasm to the center's bean breeding program, to successively find resistances to pests and diseases, adaptation to low phosphorus and drought, and more recently higher content of iron and zinc in seeds. The collection was also used to progress knowledge in biological sciences, as shown by a dozen of examples. A reason behind these successes was foresight and focus on diversity *per se* in the collection. The paper ends with a number of suggestions for the way ahead for the genetic resources conservation and management of these bean crops, and possible take-home lessons for curators in charge of other similar collections.

Keywords: distribution, yield, biotic stress, abiotic stress, breeding, *Phaseolus*

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The purpose for establishing a collection of genetic resources at CIAT

Created in 1967, the International Center of Tropical Agriculture (CIAT for its Spanish acronym) was the third international center of agricultural research whose mandate was to increase the agricultural productivity in the tropics. Because of population growth a sure food availability crisis was anticipated and yields of key staple crops had to increase (Kastner *et al*, 2012) and, fortunately, this actually happened, namely in Asia (Evenson and Gollin, 2003). Although CIAT was originally designed to improve agricultural systems in the lowland tropics (the Center had a couple of animal production programs), it became clear that the level of human talents, physical and financial resources required for such a task was beyond the donors' capacity and time frame, and these limits indicated to re-focus instead (Lynam and Byerlee, 2017). After the successful experience of the International Rice Research Institute (IRRI) in Los Baños, Philippines, on rice and that of the Centro Internacional para el Mejoramiento del Maíz y Trigo (CIMMYT) in El Batán, Mexico, on wheat, and as an outcome of international conferences (Hernández-Bravo, 1973; Rachie, 1973; Voysest-Voysest, 1983), CIAT moved from a Food Legumes Production Systems Program into a program focused on common bean, *Phaseolus vulgaris* L. (Hidalgo, 1991); the Bean Program initiated in January 1974 (Voysest-Voysest, 2000).

Given the production problems faced for this crop (Hernández-Bravo, 1973; Singh, 1992), very often managed by small-holder farmers with limited access to inputs (Broughton *et al*, 2003), the next strategic decision was to increase productivity by transferring resistance to diseases and pests into target varieties. By then, the most severe diseases, out of more than one hundred affecting the crop (Zaumeyer and Thomas, 1957; Singh, 1999), often caused a 70-100% loss in yield (Sanders and Schwartz, 1980; Singh, 1999). The first cycle of breeding (which took about 8-10 years in beans in the 1960s) aimed at securing the potential yield of the landraces (Rachie, 1973). Thus, farmers would have a secure food stock at home and a surplus for

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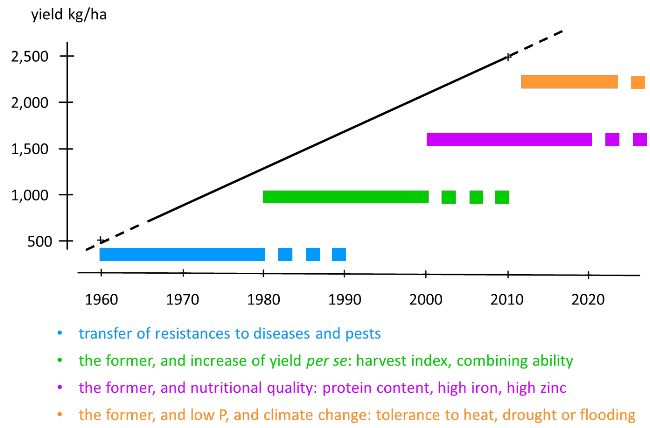

Figure 1. Evolution of the breeding strategy in bush common bean in the tropics over the last decades.

sale in local markets. This strategy was likely to work because in subsistence agriculture beans were planted in mixtures to where resistant genotypes would lower the disease pressure for the total crop (Clawson, 1985), and in market-oriented agriculture with fewer genotypes under cultivation a higher part of the production would be saved for sale.

It was envisioned to tackle the next most limiting factor to productivity in a cumulative way, through the production and distribution of elite varieties, with the active participation of the national partners, who then would work with extension services for the diffusion of such a technological package. That participation was critical for impact, given the high number and regional variation of commercial seed types (Voysest-Voysest, 1983; Voysest and Dessert, 1991). Figure 1 shows how this strategic approach has worked for common bean over five decades. With each breeding cycle tackling a new challenge, the strategy had to be cumulative, because the entire production chain and the final users would hardly accept to go backwards. In this regard, it is worth noting that after fifty years, diseases and pests continue to be among the highest priorities of bean breeding, especially in Africa (Assefa *et al*, 2019).

While the first breeding cycle was under way, improvements were introduced to agronomical practices, taking into account planting density, planting date versus water availability versus solar radiation/photoperiod, minimum of nitrogen-phosphorus-potassium fertilization, or pH correction by lime application (Thung, 1991). Once these improved agronomical practices were implemented, it was clear that progress in yield had to come from plant breeding (Borlaug, 1983), but there was a critically important assumption for the whole strategy to work: the immediate availability of well characterized and evaluated genetic resources, which would be the ultimate source of all desirable genes. Practically, because there were none at the Center, this meant assembling large collections of genetic resources of beans and evaluating such collections by multidisciplinary teams. In the early years of CIAT, that assumption had to quickly become reality for the efficiency and impact of the breeding efforts. The need for multiple sources for disease and pest resistance and abiotic stress tolerance was also related to the wide diversity of conditions of deployment in the many countries benefiting from that technology. Note that apart from assembling collections, it was also the time of setting the founding principles of genebank management (Allard, 1970; Frankel and Hawkes, 1975).

How the *Phaseolus* collection was assembled

With the establishment of the CIAT Bean Program, the first introductions of bean collections from other institutes (e.g. United States Department of Agriculture [USDA], Pullman, USA; Instituto Nacional de Investigación Agrícola, Chapingo, Mexico; Instituto de Ciencias y Tecnología Agrícola, Chimaltenango, Guatemala; Centro Agronómico Tropical de Investigación y Enseñanza [CATIE], Turrialba, Costa Rica) (Hernández-Xolocotzi, 1973; Vieira, 1973) were made thanks to the constant cooperation of the Instituto Colombiano Agropecuario, Palmira, Colombia on plant quarantine matters (Figure 2). Accessions were registered as Germplasm numbers (e.g. G4017 for ‘Carioca’, perhaps the most planted bean variety in the world; Voysest-Voysest (2000). Thanks to the support of the International Board for Plant Genetic Resources (IBPGR), Rome, Italy (established in 1974), several collecting missions were organized for landraces and wild species. Before the entry into force of the Convention on Biological Diversity (CBD), these crop genetic resources were considered as common heritage of humankind, and there was free exchange of genetic resources for breeding and agricultural research purposes. After December 1993, acquisition by introduction of copies of germplasm collections and explorations came to a halt (as experienced in other genebanks of the Consultative Group on International Agricultural Research (CGIAR); Halewood *et al* (2020). But in recent years, target explorations were carried out under the legal framework set by the International Treaty on Plant Genetic Resources for Food and Agriculture (FAO, 2002), for example in Costa Rica.

Because beans as a staple are often associated with maize, collections of bean germplasm have been established across the tropics and subtropics, particularly in Latin America (e.g. in Chapingo in Mexico, Medellín in

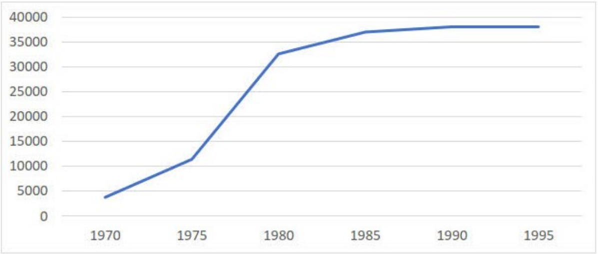

Figure 2. Increase in size of the bean collection introduced into the CIAT genebank.

Colombia or Campinas in Brazil) (Vieira, 1973), which could be introduced into CIAT. It was not rare for a maize breeder to pick up seeds of local bean landraces when visiting a farmer or a local market and give them to colleagues in charge of bean breeding. As a general practice in Latin America the maintenance of bean germplasm collections was a side activity of the bean breeders. Given this kind of attention, it is no surprise that the landraces of the market classes worked on by the breeders were well represented in the respective collections. Retrospectively, this is positive because some of these collections were made in the 1940-1960s, just before massive rural transportation blurred the origins of many local landraces. By that time, the varieties selected or bred over the last decade were starting to replace many landraces. This replacement was seen in small black and red-seeded bean varieties of Central America. Consequently, the most original genetic variation in landraces that existed in the 1940s is by now either in genebanks or lost. Collecting today will only result in duplicates or in samples of bred materials.

The focus on common bean and the need to find resistances for several market classes of beans as final targets influenced the makeup of the collection (Table 1). As the Bean Program was working with Central American countries and Brazil (Voysest-Voysest, 1983), many small-seeded collections were introduced, but because CIAT also worked together with Andean countries, large-seeded collections were included as well (both collections but particularly the last ones were important for Africa: Martin and Adams (1987). Cultivated *P. vulgaris* makes up the biggest part of the collection, the other cultivated species follow, with a total of 32,183 landraces and 2,797 improved varieties. The wild forms of the cultivated species and the wild species are represented by over 2,000 accessions (Table 1).

The number of country depositors is 110. The top five countries that have contributed most are: Mexico (6,237 accessions), Colombia (3,927 accessions), Peru (3,798 accessions), Guatemala (2,853 accessions) and the United States (1,863 accessions), followed by Brazil, Ecuador, Turkey, Malawi and Costa Rica (with around 1,000 accessions each). Restoration of national bean diversity has been done for Bhutan, Chile, Costa Rica, India, Iran, and Mexico, based on institutional agreements.

After partial safety duplications at CATIE and Centro Nacional de Pesquisa de Recursos Genéticos e Biotecnologia, Brasilia, it was decided in 1996 to make a complete backup at CIMMYT because extra space was kindly offered by Bent Skovmand then in charge of the wheat collection. This included a check for viability and absence of diseases of quarantine importance. By 2019, 92% of the bean collection had been safely duplicated at CIMMYT. When the Global Svalbard Seed Vault (GSSV, Longyearbyen, Norway) was opened in February 2008 (Fowler, 2016), a second safety backup was implemented there. By 2019, 94% of the bean collection was safely duplicated at GSSV. In addition, CIAT safeguards in its vault the seed backups of the food legume collection of the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria, and the tropical forage legumes of the International Livestock Research Institute (ILRI), Addis Ababa, Ethiopia.

Table 1. Accessions of the in-trust *Phaseolus* collection kept at CIAT Palmira (information also available in Genesys: https://www.genesys-pgr.org/a/overview/v2ZW8lQwlep)

Species	Biological status	No. accessions
P. vulgaris, common bean	cultivated (landraces, commercial varieties)	30,571
	wild and weedy forms	1,804
P. lunatus, Lima bean	cultivated (landraces, commercial varieties)	3,031
	wild and weedy forms	274
P. coccineus, scarlet runner	cultivated (landraces, commercial varieties)	760
	wild and weedy forms	198
P. dumosus, year-bean	cultivated (landraces)	475
	wild and weedy forms	15
P. acutifolius, tepary	cultivated (landraces, commercial varieties)	161
	wild and weedy forms	165
Other species (41[1])	wild forms only	484

[1] This figure represents half of the number of species of the genus (Debouck, 2021).

The diversity in the bean collection and its use

Given the breeding priorities (Figure 1), the bean collections were evaluated by multidisciplinary teams in multiple locations in Colombia, first in Palmira, in Quilichao since 1977 and in Popayán since 1978 (Cuellar, 2003). Resistances to several highly damaging diseases (e.g. anthracnose, angular leaf spot (ALS), bean common mosaic virus (BCMV), rust) were found (Table 2) and transferred as their mode of inheritance was progressively defined (Singh, 1992; Beebe *et al*, 1997; Beebe, 2012). However, bean breeders soon realized that further genetic progress would be obtained only by screening the diversity outside the respective market classes, and that for many traits (e.g. *Ascochyta* blight, bean golden mosaic virus (BGMV), bean golden yellow mosaic virus (BGYMV), common bacterial blight, halo blight, web blight, white mold, bruchids and leafhoppers) there were very few or no sources of workable resistance (Miklas *et al*, 2006; Singh and Schwartz, 2010; Beebe, 2012). In a copy of the USDA collection there were a few accessions of wild common bean from Mexico collected in the 1960s by Howard Scott Gentry in which, later on, César Cardona and his team found bruchid resistance associated with a particular seed protein (Osborn *et al*, 1988). The screening for the right variants of that protein by electrophoresis opened the way for marker assisted selection (Kelly and Miklas, 1999), widely applied in breeding for BGYMV resistance (Broughton *et al*, 2003), anthracnose resistance (Kelly, 2004) and other traits. The wide secondary gene pool (e.g. *P. coccineus, P. costaricensis, P. dumosus*) has just started to be evaluated, and has already shown promise against *Ascochyta* blight (Schmit and Baudoin, 1992), angular leaf spot (Mahuku *et al*, 2003) and white mold (Singh *et al*, 2013). Such resistances were expected because the species of the section *Phaseoli* thrive in montane humid forests (Debouck, 2000) where these fungi diseases are frequent selection pressures (Cattan-Toupance *et al*, 1998) and have likely been present over hundreds of thousands of years, given the age of these species (approximately 1 million years) (Delgado-Salinas *et al*, 2006; Rendón-Anaya *et al*, 2017).

Once disease resistances were transferred to the preferred varieties in the different market classes, yield came as the next challenge, in order to keep bean as a competitive (mono-)crop as compared to soybean, cowpea or sorghum. An early approach, in line with the spirit of the Green Revolution in wheat (Donald, 1968), was to optimize the ideotype under favorable environments (Adams, 1973). That breeding effort on plant architecture continued (Kelly, 2001), although with limited success in the tropics (Beebe, 2012). An important outcome, however, has been the rise of growth habit 2 or bush erect indeterminate (race 3 of Evans (1973) for mechanical harvesting in bean improved germplasm, little present in traditional landraces of Latin America. This also offered opportunities to enrich the collection (Hidalgo *et al*, 1992). Another breeding goal was to combine the productivity of the small-seeded varieties with the grain size of the large-seeded ones, many of them demonstrated to be of Mesoamerican and Andean origin, respectively (Evans, 1976). Thus came the works evidencing the two major gene pools (Gepts *et al*, 1986; Singh *et al*, 1991b; Kwak and Gepts, 2009; Bitocchi *et al*, 2013), and the races within them (Singh *et al*, 1991a; Beebe *et al*, 2000b; Blair *et al*, 2007, 2012). The presence of races was a bit unexpected in an autogamous crop but could be explained by the role of outcrossing during early domestication (Chacón-Sánchez *et al*, 2021). Some genetic isolation and poor recombination have been shown to exist between the two major genepools (Singh and Gutiérrez, 1984) and since the wild state (Koinange and Gepts, 1992). But significant heterosis was demonstrated to exist (Nienhuis and Singh, 1986; Bannerot, 1989), especially between races (Singh *et al*, 1993; Singh and Urrea, 1995), while genetic disorders between races were sometimes observed (Singh and Molina, 1996). The significant interactions with the environment, however, have resulted in a narrow commercial applicability of this approach (Gutiérrez and Singh, 1985; Nienhuis and Singh, 1986). Another strategy inspired from the quantitative developments in tomato breeding (Tanksley *et al*, 1996) was the advanced backcross QTL analysis using a wild form. The accessions of wild *P. vulgaris* G12947 (Acosta-Gallegos *et al*, 2007), G19892 (Buendía *et al*, 2003), G24404 (Blair *et al*, 2006) and G24423 (Kelly, 2004) were found to contribute a significant QTL for yield (a 27% increase as compared to the recurrent parent in the last example). In some cases, the use of weedy types would help reduce the number of backcrosses needed to recover the appropriate seed size (Acosta-Gallegos *et al*, 2007). Another innovative approach has been the use of lines coming from crosses with the year-bean (for transfer of high iron in the grain) or with tepary (for transfer of bacterial blight resistance) in order to bring more monocarpism into common bean (Klaedtke *et al*, 2012; Mejía-Jiménez *et al*, 1994). The bean crop with exceptions in growth habits 1 and 2 still has the ancestral trait of continuing shoot production and lateral flowering, while the first pods already enter into maturity. In the wild it makes all sense, but not in a crop aimed at mechanical harvesting. The desert ephemerals of the genus such as *P. acutifolius* A. Gray, *P. filiformis* Benth, or *P. microcarpus* Mart. (Freytag and Debouck, 2002) invest much less in profuse branching but soon move all photosynthesis products into their seeds. Thus, under heat or drought stress, it makes sense to quickly redirect such products to the only part that will be harvested (Rao *et al*, 2013; Suárez *et al*, 2020).

One outcome of the increase in size of the collection and the first phase of germplasm evaluations at CIAT was the establishment of core collections (along the concept introduced by Frankel and Brown (1984). The CIAT common bean core collection was established by use of Geographic Information Systems maximizing the environmental diversity of landraces, and a few morpho-agronomic descriptors (Tohme *et al*, 1995a). The core collection, consisting of 1,556 accessions, has been used for the identification of germplasm tolerant to low phosphorus (Beebe, 1997) or containing high levels of micronutrients (Islam *et al*, 2002). For both traits less than 10% of the total collection had been evaluated at that time (Beebe *et al*, 2000b,a), explaining the recourse to the core collection. Using core collections was, in part, the consequence of internal duplication or redundancy in general collections, which for cultivated common bean has been estimated at 50% across the major genebanks (Lyman, 1984). This figure is perhaps on the high side but reflects the amount of commercial and breeding materials kept in genebanks as compared to primary sources of variation (landraces, wild species). As mentioned, the management of germplasm collections was often a side activity of bean breeders who would hesitate to eliminate all variants close to the target market class. Given the cost of keeping accessions versus the cost of tracking down internal copies (this was then achieved by multi-site characterization, in addition to passport data) (Koo *et al*, 2004), the problem was not given high priority in the past. With the development of SNP genotyping technology, this issue should be revisited,

Table 2. Bean accessions from the CIAT collection used as sources of resistance to diseases and pests.

Trait	Material used	References
Diseases		
angular leaf spot	G10613 from Guatemala	Pastor-Corrales *et al* (1998)
	interspecific hybrids with *P. coccineus*; G4691	Pastor-Corrales *et al* (1998); Islam *et al* (2002); Mahuku *et al* (2003)
angular leaf spot and anthracnose	G3991 from Costa Rica	Schwartz *et al* (1982)
anthracnose	Aliya G02333	Young and Kelly (1996)
	Kaboon G1588; Cornell 49-242 G5694	Melotto and Kelly (2000)
	interspecific hybrids with *P. coccineus* G35252	Mahuku *et al* (2002)
Ascochyta blight	*P. dumosus* G35369 from Costa Rica	Schmit and Baudoin (1992)
	P. dumosus G35182 from Guatemala	Garzón *et al* (2011)
bacterial wilt	wild *P. vulgaris* G12883 from Mexico	Urrea and Harveson (2014)
Bean Golden Yellow Mosaic Virus (BGYMV)	*P. coccineus* G35172 from Rwanda	Beaver *et al* (2005)
Bean Common Mosaic Virus (BCMV)	Porillo Sintético G04495, Royal Red G04450	Singh *et al* (2000)
beet curly top virus	California Pink G06222, Red Mexican G05507	Larsen and Miklas (2004)
	Porillo Sintético G04495, Burtner, Tio Canela 75	Singh and Schwartz (2010)
common bacterial blight	interspecific hybrids with acutifolius VAX4, MBE7	Zapata *et al* (1985); Singh and Muñoz (1999); Michaels *et al* (2006); Navabi *et al* (2012)
	Montana No. 5; PI 207262	Miklas *et al* (2003, 2006)
halo blight	Montcalm G06416, ICA Tundama G14016	Beaver (1999)
	Palomo G12669	Schwartz (1989)
	Pinto US 14 G18105	Singh and Schwartz (2010)
	Wis HBR 72 G03954	Taylor *et al* (1996)
Fusarium root rot	Porillo Sintético G04495; wild *P. vulgaris* G12947	Beebe *et al* (1981); Acosta-Gallegos *et al* (2007)
Pythium root rot	PI 311987 G02323	Beebe *et al* (1981)
Rhizoctonia solani rot	N203 G00881	Beebe *et al* (1981)
rust	Compuesto Negro Chimaltenango G05711	Stavely (1984)
	Ecuador 299 G05653	Stavely and Pastor-Corrales (1989)
	Redlands Pioneer G05747	Liebenberg *et al* (2006)
	PI 260418	Singh and Schwartz (2010)
web blight	BAT 93; Flor de Mayo G14241	Beaver *et al* (2002)
white mold	*P. coccineus* PI 175829 from Turkey	Abawi *et al* (1978)
	P. dumosus PI 417603 from Mexico	Hunter *et al* (1982)
	interspecific hybrids with *P. coccineus* G35172	Singh *et al* (2009)
	interspecific hybrids with *P. costaricensis* G40604	Singh *et al* (2013)
Pests		
Acanthoscelides weevil	wild *P. vulgaris* from western Mexico G12952; QUES	van Schoonhoven *et al* (1983); Zaugg *et al* (2013)
Apion godmani pod weevil	Amarillo 154 G03982; G03578	Beebe *et al* (1993); Garza *et al* (2001)
Empoasca leafhoppers	Turrialba 1 G03712	Galwey (1983)
	California Dark Red Kidney, from USA G17638	Schaafsma *et al* (1998)
Ophiomyia bean fly	*P. coccineus* G35023 and G35075, and interspecific hybrids	Kornegay and Cardona (1991)
whiteflies Aleyrodidae	DOR 303	Blair and Beaver (1992)
Zabrotes weevil	wild *P. vulgaris* from Chiapas, Mexico G24582	Acosta-Gallegos *et al* (1998)

with the merging of near identical accessions and the review of the core collection (as already suggested for the USDA core collection by Kuzay *et al* (2020). The most significant costs ahead are likely to be about regeneration and evaluation, not the chasing of internal copies helped by robotics!

Distribution of the bean collection

Since being established in August 1977 as an internal service unit (Hidalgo, 1991), the genebank has distributed to the Bean Program and the Biotechnology Research Unit of CIAT a total of 318,148 samples (or 69.4 % of the total distributed) (Figure 3). Externally, the genebank has distributed 140,109 samples (or 30.6% of the total) to users in 105 countries. The total distributed was 458,257 samples of 37,657 accessions, or 99% of the bean collection. These figures indicate that: i) the collection has been studied and used initially by the scientists of CIAT, ii) the number of countries benefiting from the conservation work through distribution almost matches with the number of country depositors, and iii) the collection has been distributed almost entirely (this percentage could be even higher since some accessions have not been distributed due to lack of seeds). One should note that apart from CIAT programs, the most important users were national agricultural research services, universities and research institutes. The shares of farmers, commercial companies and non-governmental organizations in the distribution were low in comparison. Assuming farmers are aware of the existence of germplasm collections, reasons for the low number of requests might be related to the farmers' access to on-line request processes (mail requests were honored), as well as the capacity to deal with phytosanitary regulations in the respective countries. As dry bean breeding has been mostly carried out by public institutions, requests of genetic diversity by the private sector were few, often related to specific sources of variation for snap bean breeding (e.g. sources of resistance to anthracnose).

The purposes of distribution have generally followed the breeding priorities shown in Figure 1: interest in resistances to diseases and pests, nutritional quality and more recently tolerance to abiotic stresses such as drought and high temperature. As discussed below and shown in Figure 4, a significant part of the distribution has been for the purpose of advancing knowledge. In Figure 4, breeding activities (38.9%) and applied research (e.g. in pathology or entomology: 37.1%) were the top purposes for seed requests, followed by agronomy (11.7%) and basic research (e.g. in genetics or evolutionary studies: 9.6%). The variation in number of distributed samples from one year to another can be significant, namely if the core collection with over 1,500 accessions was requested and sent. The peak in distribution in the period 1978-1996 practically matches with that of the activities of CIAT Bean Program (Voysest-Voysest, 2000). For the period 1973-2019, the top five recipient countries were: USA (26,093 samples), Colombia (18,444 samples), Brazil (9,198 samples), Guatemala (7,430 samples) and Mexico (6,787 samples). The term 'samples' is preferred over 'accessions' as a country recipient could ask for a specific accession more than once.

Apart from germplasm, the genebank also distributed information related to the in-trust collections. An indicator of this service is given by the number of consultations of the genebank website (https://ciat.cgiar.org/what-we-do/crop-conservation-and-use/) to have access to data (Figure 5).

Statistics about access to genebank information and services in recent years show that most of the visitors (81%) reach the genebank website directly, indicating a user knowledge and confidence that relevant information can be found there, while 19% of visitors find the website through a browser search or are referred to it through another link. Users also benefit from specialized technical information currently consisting of 658 documents (including articles, book chapters, conference proceedings, germplasm exploration reports, posters and presentations). These documents can be accessed through the genebank website or the institutional document repository CGSpace (https://cgspace.cgiar.org/handle/10568/35697), that registered 27,278 downloads in 2017-2019.

Impact of the bean genetic resources collection

The 225 varieties released in 17 countries of Latin America and the 88 varieties released in 14 countries of Africa in 1974-1999 by the Bean Program (Voysest-Voysest, 2000), the check of BGYMV in Central America (Beebe, 2012), as well as the yield gain from 688 kg/ha to 782 kg/ha in eastern Africa (Lynam and Byerlee, 2017) eventually have their origin in the CIAT genebank. Once the interesting traits were identified (Table 2); (Hidalgo and Beebe, 1997), through different breeding schemes, elite varieties were produced, tested and released via international nurseries such as the International Bean Yield and Adaptation Nursery (Voysest-Voysest, 1983; Beebe, 2012), generating significant economic and social benefits (Johnson *et al*, 2003). In this last work, over the period of analysis, and because of the varieties involved, some countries of Latin America and the Caribbean were net beneficiaries (Argentina, Brazil), while others were net contributors (Mexico, El Salvador). Overall, and over the duration, however, it seems that all countries benefit from conservation and unrestricted international exchange of germplasm (Johnson *et al*, 2003).

As an example of changing context over time, the gene *gy.* originating from Peru and conferring an intense and sustained yellow color (Bassett *et al*, 2002) was used since 1978 in northwestern Mexico (Lépiz-Ildefonso and Navarro-Sandoval, 1983), because it gave a premium price as compared to the fading color in yellow-seeded traditional landraces. It ended up in the variety 'Azufrado Peruano 87' (Voysest-Voysest, 2000) and also

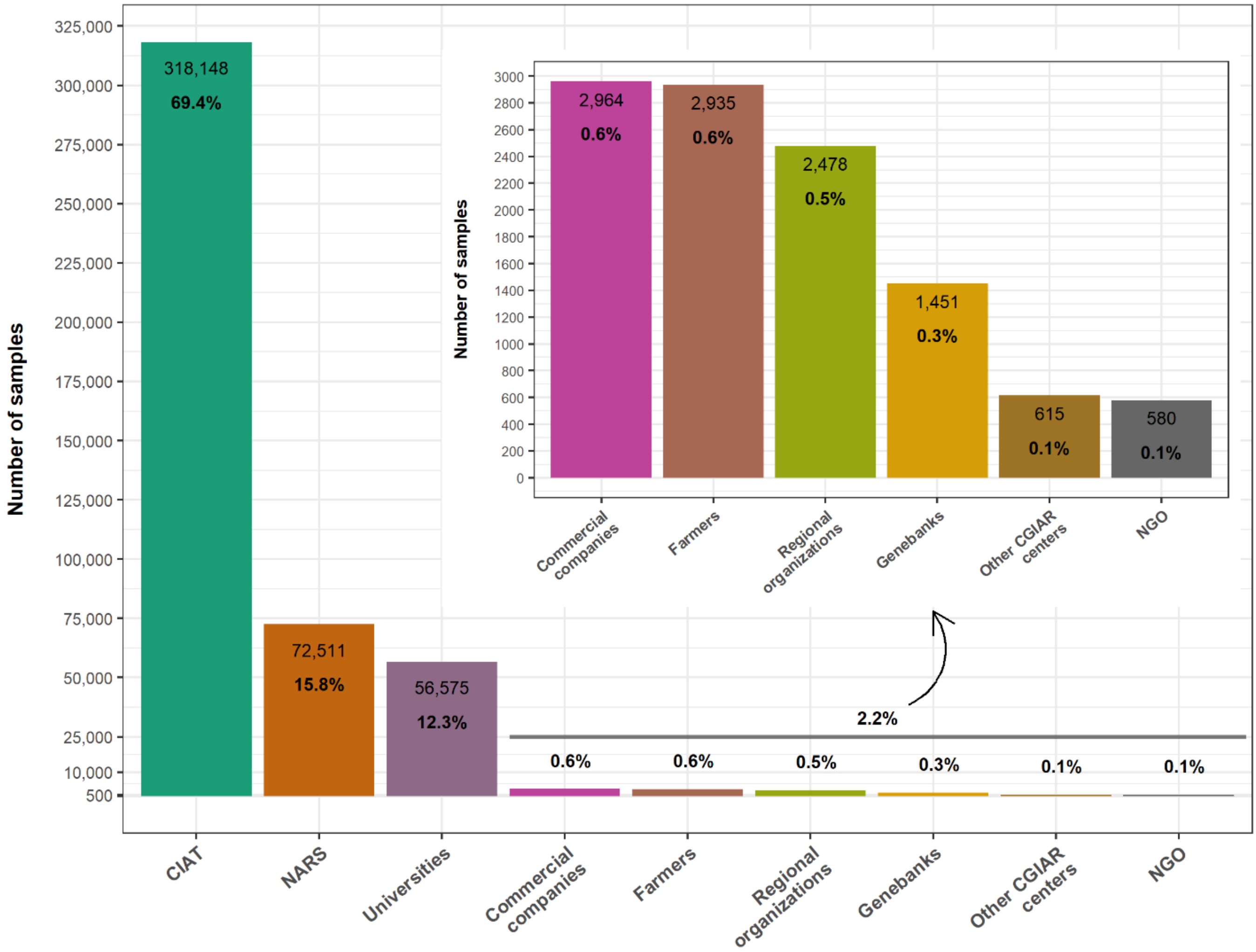

Figure 3. Number of samples distributed in the period 1973-2019. Important recipients were the Bean and Biotechnology Programs of CIAT, the national agricultural research services (NARS), universities and research institutes.

an undue patent granting (genetically dissected in great detail by Pallottini *et al* (2004). It is because the in-trust collection was rich in yellow-seeded accessions from Mexico and Peru, and because the CIAT genebank kept past records such as old catalogs of varieties (Hedrick, 1931), it was possible to demonstrate ample prior art, and the patent was turned down in 2008.

Legumes have been called the ’meat of the poor’ (Heiser, 1990) and in many parts of Latin America (e.g. Brazil, Mexico, Cuba) people with low income eat beans daily. Similarly, the highest consumption rates per capita are currently registered in eastern Africa (OECD, 2015). Given this, it was becoming evident that improved varieties should also fight the ‘hidden hunger’ or the deficiency in minor minerals such as iron and zinc where the diet is not sufficiently diverse. Using the core collection, the evaluation to find accessions with high iron and zinc was expanded (Islam *et al*, 2002), and good sources were identified (G21242, G23818, G23834) (Blair *et al*, 2011), primarily from the Andean region. Nothing on the seed aspect indicates high values in these micronutrients. Likewise, G14519, an old landrace named ‘Hickman Pole Bean’ from the United States and belonging to the Mesoamerican genepool, also has shown potential (Blair *et al*, 2010). From the start, the genebank had interest in assembling variation for any future need, and this is precisely the wide scope that made biofortification possible thirty years later and with a lasting impact where it is today most needed, e.g. in East Africa (Sellitti *et al*, 2020).

With changing context of bean production over the last forty years, for example, common bean being pushed towards the west in the Plains of the USA or in the Canadian prairie, the northwest in Mexico and the northeast in Brazil (Singh, 2001), new challenges like drought, cold, heat or low phosphorus are set for breeding. Some drought tolerance can be found in the ‘Durango’ race (Singh, 2007; Beebe *et al*, 2013), in other landraces such as G21212 (Beebe *et al*, 2008) and in wild forms (Cortés and Blair, 2018). Root architectural and physiological traits identified in an Andean landrace, G19833, may contribute to phosphorus acquisition (Beebe *et al*, 2006).

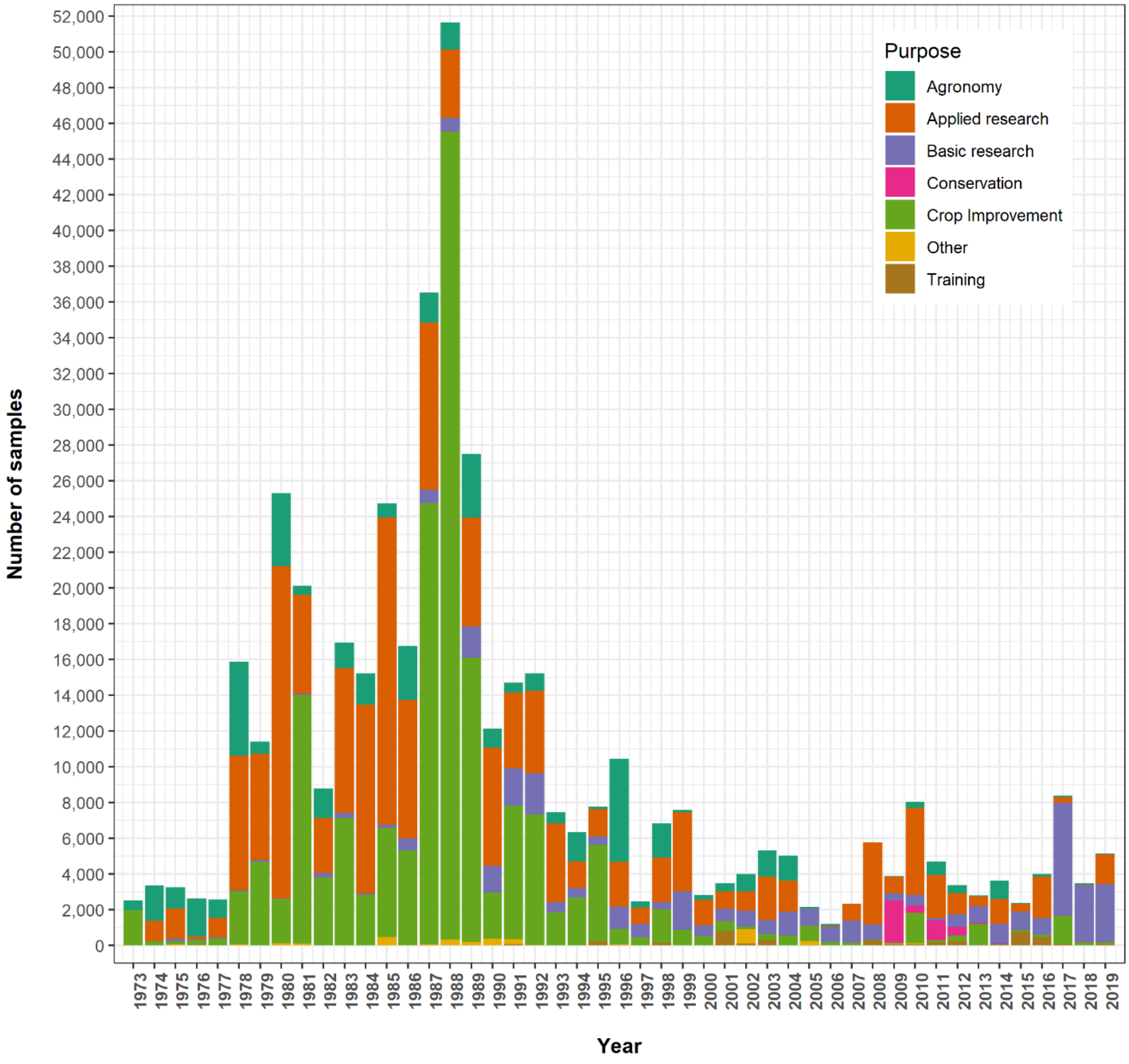

Figure 4. Number of samples distributed annually to users in the period 1973-2019, according to the purposes of requests.

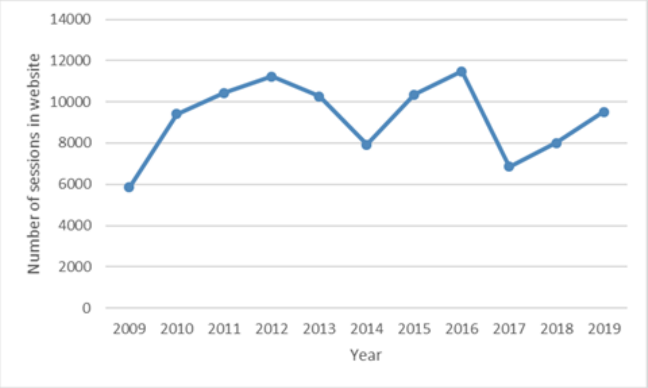

Figure 5. Number of consultations of the CIAT genebank website (https://ciat.cgiar.org/what-we-do/crop-conservation-and-use/) in the period 2009-2019.

The impact of the bean germplasm collection has also been through the direct adoption of genebank accessions by farmers after the screening of international nurseries. No less than thirty-four accessions have been registered in national catalogs of varieties in thirty-eight countries in 1974-1999 (Voysest-Voysest, 2000), or 13% of the total of improved genetic materials distributed by CIAT. This figure may not look impressive, but bean varieties produced by breeding have been released in the same geographic areas since the 1940s. That said, it is anticipated that apart from the use of landraces for specific niche markets (see popping beans below), for specialized studies for example in pathology (e.g. disease differential sets) or for servicing gardeners, a significant coming impact of genetic resources will materialize through libraries of genetic stocks (van

Treuren and van Hintum, 2014), targeted diversity panels (Cichy *et al*, 2015; Moghaddam *et al*, 2016), and sequence tagged traits (Lobaton *et al*, 2018). But in order to allow the 'molecular' breeder to do advanced searches throughout the collection substantial changes must be brought to databases (McCouch *et al*, 2012; Byrne *et al*, 2018). Learning from experience, the design should be for use by non-database experts, modular and scalable, moving from passport data into accession traits and ending into annotated genes. Somehow, this focus re-emphasizes the role of genebanks as keepers of the primary genetic variation, and perhaps less of all allelic combinations of that variation (i.e. the sister lines of simple crosses), since tools now exist to recombine that variation to better meet human needs or agricultural contexts (towards precision agriculture for instance). Appraising that variation by curators might be difficult (what should be kept in the genebank remains a cornerstone and recurrent question), although they will be helped by sequence information. From a pragmatic perspective genebanks may keep interest in old landraces since these have been tested over long durations in farmers' fields. For similar efficiencies in breeding, genebanks might be interested in keeping recombinants between gene pools, for example from southern Europe (Gioia *et al*, 2013), part of the Guarani area in Brazil (Burle *et al*, 2010) or the northern Andes (Chacón-Sánchez *et al*, 2021), especially if they represent novelties in agronomic or nutritional attributes.

The other impact: the contribution to knowledge

The in-trust collections, because of the open access set forth by FAO in the early years and then the facilitated access approved by the parties to the International Treaty (FAO, 2002), have helped increase knowledge in many fields of biological sciences (Dudnik *et al*, 2001). Conversely, the increased knowledge contributed tremendously to the efficiency of the breeding and varietal deployment efforts. This was particularly applicable to the mandate crops of CIAT, since with the exception of rice, not much basic biology and genetics was known in the late 1960s when crop improvement efforts were launched. For instance, the ancestry of common bean became firmly established at a time not far away from the founding of CIAT (Burkart and Brücher, 1953; Gentry, 1969). The double domestication of common bean became obvious only in 1986 (Gepts *et al*, 1986), and that of Lima bean in 1989 (Debouck *et al*, 1989), and the existence of a fifth case of domestication in the genus was clarified as late as 1991 (Schmit and Debouck, 1991)!

Such increased knowledge also helped to better define what should be conserved in genebanks; for example, studies on the founder effect due to bean domestications have stressed the importance of wild forms for accessing the total genetic diversity of three bean crops (Sonnante *et al*, 1994; Martínez-Castillo *et al*, 2015; Mina-Vargas *et al*, 2016). As expected, that founder effect was less marked in the scarlet runner (Guerra-García *et al*, 2017). That knowledge also helped in the development of disease indexing methods for the safe movement of germplasm (Kumar *et al*, 2021). Some examples are provided in Table 3 (by tracking accessions distributed in 1973-2019). The breadth of disciplines, evidenced by the diversity of peer-reviewed journal titles and linked to genebank accessions, is striking but just reflecting the diversity of the collection. No less important are the opportunities of scientific collaborations around 'problems' set up by the bean crops and materials provided by the genebank, as reflected by the institutions and countries of authorships.

Knowledge often overlooked, although associated with crop germplasm for millennia

Because germplasm collections were assembled at CIAT primarily in relation to breeding, traditional knowledge associated with specific accessions was rarely documented. As the first phase of breeding was focused on resistance to diseases and pests, with systematic inoculation of known strains, there were often no incentives for a time-consuming effort to document vernacular names, culinary and other folk practices. One such example is that of popping beans consumed toasted (National Research Council, 1989). That group of landraces still exists in the Andes, from Cajamarca in Peru down to Chuquisaca in Bolivia (Tohme *et al*, 1995b). Elder farmers in the countryside will tell which variety can pop, while migrants to urban areas one generation after will simply process them all in water cooking, even with a slight increase in digestibility (van Beem *et al*, 1992). Documenting this property by the genebank is doubly important. First, consumer preferences change over time (Voysest-Voysest, 2000) and, in contrast to the 1960s, there is a renewed interest nowadays in local gastronomy that can provide a better income to mountain farmers (Zimmerer, 1992). Second, water and fossil energy might become expensive inputs to food processing or transportation, as it is still the case in many parts of rural eastern Africa. In pre-ceramic times in the Andes, these two inputs (excepting fire) were either difficult to carry or to access. Producing a hot surface with the help of solar energy might not be an excessively difficult or expensive technology to implement in the Andes or in eastern Africa. In altitude, this kind of germplasm and the unique way to make it ready for human consumption may also contribute to reduce deforestation for fuel wood, while montane forests usually occupy a small acreage (National Research Council, 1989). Finally, it is worth noting that this group has a high number of phaseolin types (Tohme *et al*, 1995b), indicating a high diversity in contrast to other Andean landraces (Beebe *et al*, 2001). Evaluation of popping beans is continuing in Peru (Cruz-Balarezo *et al*, 2009) and Colombia (Otálora *et al*, 2006), while

Table 3. Examples of impact of CIAT bean in-trust collection for the advance of knowledge.

Field	Output, problem solved	References
Botany	new species described	Salcedo-Castaño *et al* (2011)
Plant taxonomy	taxonomic status of bean species re-assessed	Schmit *et al* (1996)
	review of the genus and species	Freytag and Debouck (2002)
Agricultural botany	founder effect of bean domestication	Schinkel and Gepts (1988)
	definition of a 3^{rd} gene pool in Lima bean	Motta-Aldana *et al* (2010)
	fifth case of domestication in the genus	Schmit and Debouck (1991)
Crop evolution	recombination between gene pools	Gioia *et al* (2013)
Phylogeography	past trans-isthmic migrations of wild bean	Chacón-Sánchez *et al* (2007)
Plant breeding	gene pools/ races of common bean defined	Singh *et al* (1991a)
Plant pathology	inheritance of ANT/ALS resistance genes	Gonçalves-Vidigal *et al* (2011)
	coevolution of ALS in bean gene pools	Guzmán *et al* (1995)
Plant virology	resistance to Clover yellow vein virus	Hart and Griffiths (2014)
Entomology	resistance to bean bruchids	Cardona *et al* (1990)
	resistance to bean weevil	Kamfwa *et al* (2018)
Plant genetics	common bean genomic map	Schmutz *et al* (2014)
	common bean genome history & evolution	Rendón-Anaya *et al* (2017)
	inheritance of pod dehiscence	Parker *et al* (2020)
	inheritance of leaf mutation	Garrido *et al* (1991)
Plant biotechnology	genetic transformation in tepary bean	Dillen *et al* (1997)
Plant physiology	flowering response to daylength	White and Laing (1989)
	identification of phosphorus-efficient genotypes	Beebe *et al* (1997)
	low phosphorus tolerance in bean	Rao (2001)
	variation in photosynthetic activity	Lynch *et al* (1992)
Plant root physiology	tolerance to NaCl salinity in early growth	Bayuelo-Jiménez *et al* (2002)
Plant microbiology	coevolution of *Rhizobium etli*	Aguilar *et al* (2004)
Human nutrition	content in micronutrients such as iron	Beebe *et al* (2000a)
	phaseolin type and digestibility	Montoya *et al* (2008)
Archaeology	crop domestication and ancient diet	Piperno and Dillehay (2008)
Intellectual Property Protection	rebuttal of an undue crop utility patent	Pallottini *et al* (2004)

the inheritance of the trait is being investigated (Campa *et al*, 2011; Yuste-Lisbona *et al*, 2012).

Serving the breeders community and beyond

As shown in Figure 3 and Table 3, distribution has been significant to a high diversity of users, going beyond CIAT breeding activities in Colombia and in eastern Africa. The trend that in some countries dry bean consumption is declining (Khoury *et al*, 2014) (contradictory to health and global environment benefits: Foyer *et al* (2016) may mean fewer requests for that kind of germplasm but an increased interest into snap bean, often of Andean origin (Myers and Baggett, 1999). With the development of urban gardening, snap bean might be on the rise, either through the planting of old heirloom varieties (Kaplan and Kaplan, 1992; Zeven, 1997) or new ones. In CIAT, the priority was on dry bean, little on snap bean for the tropics, but with possibilities of using a wide range of resistance sources developed for the former commodity (Silbernagel *et al*, 1991). The changing fate of the popping beans, even in countries of origin over the last forty years, shows the ever-changing nature of markets. Thus, examples of unpredictability abound, indicating for the genebank to focus on diversity *per se*, independently from immediate and local interests.

This example of success brings a strong message to focus scarce resources, at a time when there is risk of repeating previous work because many disciplinary continuums have been broken. Thus, it seems of paramount importance to document at accession level what is already known: phaseolin type, alleles of allozyme, RAPD markers, SCARs, SSRs, also evaluation data (trait, location, strain as applicable). Individual accessions should be linked with references and supporting documents. Keeping in mind that one third of the collection has not been evaluated, there is still a lot of work for pathologists, entomologists and virologists. Evaluations were done on up to 23,000 accessions only for anthracnose, angular leaf spot and common bacterial blight; for the other limiting pests the figures are much lower (Hidalgo and Beebe, 1997). The reaction should be reported at each accession level, and not restricted to the best performers. Evaluation should obviously capitalize on knowledge generated by previous protocols. For example, on bruchids, it is likely that evaluation of the rest of cultivated common bean germplasm will lead to nowhere (van Schoonhoven and Cardona, 1982), because domestication occurred elsewhere (Chacón-Sánchez *et al*, 2005; Bitocchi *et al*, 2013; Kwak *et al*, 2009). But the right arcelin can be picked by screening for the protein or the gene(s) involved instead of testing thousands of accessions in contact with the insects.

From previous experience, it seems likely that genebanks will face periodic shortages in skilled, highly specialized staff (a challenge also mentioned by Fu (2017). This is a recurrent limitation for germplasm evaluation (thus resulting in limited use of the collection in the future). Sending the core collection or more accessions abroad for specialized evaluations is an option, although perhaps not as fast as having it evaluated by a multidisciplinary team as done at CIAT in the 1970s. Incidentally, blocks of resistance genes (Gonçalves-Vidigal *et al*, 2020) that can be traced by molecular markers are giving an unexpected support to that approach. But in view of complex traits such as heat or drought tolerance, for which just a fraction of the entire collection has been evaluated, multi site evaluation of thousands of accessions seems extremely time-consuming and expensive. New evaluation schemes have to be designed and are a true challenge at the organ level (Zhao *et al*, 2019), but not impossible when focused for example on pulvini-caused movements of leaflets in relation to solar radiation avoidance (Thomas *et al*, 1983).

For location-related abiotic stresses, geographical approaches (targeted towards the surviving germplasm where the stress has been present for thousands of years, and thus logically the wild forms) may help. But these GIS approaches did not pick up outstanding wild forms under low phosphorus stress (eighteen accessions tested, Beebe *et al* (1997), while there seems some promise for drought tolerance (eighty-six accessions tested, Cortés and Blair (2018). Internally, these approaches requires the genebank to be strict on passport data accuracy (van Hintum *et al*, 2011). However, this is not always possible; for example, accession G40001 with promise for heat tolerance is from a market in Veracruz (Suárez *et al*, 2020). Given some intrinsic limitations of common bean, coming heat and drought stress in the tropics and subtropics (Battisti and Naylor, 2009; Beebe *et al*, 2011) may be the opportunity to re-balance the collection towards the tepary and Lima bean, more hardy crops in this regard (Freeman, 1913; Rachie, 1973), respectively). Eventually, bean breeders may realize that they have five crops instead of one, each one with a different ecological head start (Debouck, 1992). With the advances in marker assisted selection and genetic maps, it might be faster to correct a shortcoming in seed or growth habit in tepary than expecting the common bean to fully change its ecological background.

Discussion

The afore-mentioned facts suggest the following points for discussion. **First**, one can ask whether this bean germplasm collection meets the expectations for which it was established. Many sources of disease resistance were found (Table 2), and one should note that in many cases the findings were unpredicted, and largely independent of geographic origin or gene pool. As well noted by Harlan (1978), page 351) “resistance is where you find it”. For those diseases where no good sources of resistance have been found, in the light of a similar experience with the USDA collection (e.g. the case of white mold: Schwartz and Singh (2013), it seems more a deficiency of the common bean crop species itself than a severe lack of representativeness. Thus, the breeders turned logically to the wild forms and the secondary gene pools (Debouck, 1999), where the collection provided some solutions but also means for the needed preliminary studies in taxonomy and wide crossing. This links with a **second** point: given the above evidence of return on investment and incompleteness of the task (Hidalgo and Beebe, 1997), it might be important to continue with evaluation, namely for abiotic stresses such as drought or heat caused by global warming, as these will impact on yield (Lobell and Gourdji, 2012; Beebe *et al*, 2013). In view of the numbers of accessions and facing the need for developing novel evaluation schemes for abiotic stresses including a network of well characterized (climate, soil) experimental plots, it might be cost effective to cooperate with other bean germplasm repositories (e.g. Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias, Tepatitlán, Mexico; Institut für Pflanzengenetik und Kulturpflanzenforschung, Gatersleben, Germany; USDA, USA). Incidentally, this cooperation might also include a reciprocative safety backup and the development of a novel database because it is a shared concern. **Third**, to the question whether the genebank has made any impact, the answer came from bean breeding but also many actors in the global community. The figures of germplasm distribution for applied and basic research (Table 3 and Figure 4) have shown a vibrant research community worldwide adding value to the collection. They invite the genebank to a permanent capacity to respond to requests (because of the ‘on-line shopping syndrome’) but also to document these impacts. The question whether the collection will make any impact in the future should also consider technological innovations such as transgenesis and gene editing (e.g. using CRISPR-Cas9) (Doudna and Charpentier, 2014). These approaches of genetic engineering bring new light on using diversity, as they have the potential to add a new function such as herbicide tolerance or improve an existing one, such as seed protein quality, beyond the trait offer of the primary gene pool (Gepts, 2002). Transformation in common bean has proven to be particularly difficult (Jacobsen, 1999), and with limited success (Aragão *et al*, 1998, 2002; Estrada-Navarrete *et al*, 2007). Transformation seems quite possible in tepary bean (Zambre *et al*, 2005), but apparently little exploited for tepary improvement. The CRISPR technology in soybean aims at editing genes involved in a biosynthetic pathway for seed oil quality, for herbicide tolerance, or changing photoperiod sensitivity (Bandyopadhyay *et al*, 2020; Xu *et al*, 2020). New technologies will continue to appear, but under currently available evidence and costs they seem likely to contribute to a wider and/or faster use of the collection rather than to replace it. **Finally**, in this context, in order to continue to meet the broader expectations of human societies, the genebanks should fill gaps which were identified early on, in terms of geography, e.g. the northern Andes: (Hidalgo and Beebe, 1997; Beebe and Debouck, 2019); or in terms of biological coverage (Ramírez-Villegas *et al*, 2010, 2020). Wild forms and wild species should thus be better represented in the collection, with due consideration to the regeneration capacity and disclosure of the potential. There are two points here: first, given the possibilities opened by comparative mapping in the Phaseoleae (Schmutz *et al*, 2014; Vlasova *et al*, 2016; Garcia *et al*, 2021; Moghaddam *et al*, 2021) and by gene editing (Bhatta and Malla, 2020; Ku and Ha, 2020), it may be time to think beyond direct interspecific hybridization for the use of alien germplasm. In that sense, species of clade A that may represent half of the genus (Delgado-Salinas *et al*, 2006; Porch *et al*, 2013; Debouck, 2021) may be opportunities of genes to imitate and/or to regulate differently instead of genes to transfer. But given the speed of the technological development in breeding (Hickey *et al*, 2019), the action should be initiated now with the most threatened habitats (Williams *et al*, 2007), species (Goettsch *et al*, 2021), or unpredictable conditions, or time-consuming work. This leads to a second point, as forsaking millenary crops (Mamidi *et al*, 2011) does not improve humankind's food security. The four other bean crops mean four more opportunities for plant breeding. Following the diversity criteria prevailing during the establishment of the common bean collection, similar efforts should be carried out for these bean crops. The change experienced by soybean from an oriental soy sauce in North America in 1767 into an animal feeding and agro-industrial crop in just one hundred years (Hymowitz and Bernard, 1991) is a strong message to not lose options. Along the concept of a societal insurance provided by crop genetic resources (Gepts, 2006), keeping more crops alive goes in line with productive, sustainable and locally adapted agriculture and, as a consequence, with reducing rural poverty and increasing appreciation towards indigenous cultures. More than ever before, genebanks should continue to be the reserve of all options.

Concluding remarks

Figure 1 presented breeding challenges in Latin America in a time sequence, which were largely met by use of genetic resources assembled and evaluated over the last fifty years. The same germplasm collections allowed inheritance studies and the improvement of bean breeding methods, when looking for combining ability, tolerance to abiotic stress or tagging a resistance. The coming storms in areas of bean production (e.g. increased demand due to demography in eastern Africa, extinction of crop wild relatives in Mesoamerica, drought in 60% of bean growing areas worldwide) are resetting the timing to meet all breeding challenges at once and soon, but they also involve the genebanks to have the genetic solutions ready on the shelf or on the screen (or both). The contributions of the bean collections to advance knowledge on the nature, structure and evolution of *Phaseolus* genetic resources can now help the genebanks to check two extinctions: the extinction of populations in the wild, and the extinction of knowledge about cultivated diversity. Buying time on these two fronts will be difficult for genebanks, but the continuing improvement of conservation methods and efficiencies will contribute to find and enable the human talents for these daunting tasks. The above history shows many ways forward to ensure global food security in uncertain times.

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Author contributions

DGD conceptualized and wrote the paper. DGD collated the data about use and impact for the first period of the genebank, while MS covered the most recent period. LGS compiled the data about germplasm distribution. MS and LGS re-checked the data of accession numbers. All authors read, revised and approved the manuscript.

Conflict of interest statement

The first author has been responsible of CIAT genebank, as Head of the Genetic Resources Unit (1996-2009) and as Leader of the Genetic Resources Program (2009-2016), with over seventy Staff members operating in five experimental stations and three labs, for three germplasm collections (bean, cassava and tropical forages) of over 67,000 accessions. The second author has been responsible for all genebank operations in 2017 to date, which include the regeneration of bean and tropical forages collections in the experimental stations and the conservation in the labs. The third author has been responsible since 2009 for all operations related to seed conservation of the bean and tropical forages collections, which include germplasm distribution.

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Teak genetic diversity in Ghana shows a narrow base for further breeding and a need for improved international collaboration for provenance exchange

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Abstract: We evaluated the genetic diversity of teak (*Tectona grandis* L.) provenances at a newly established provenance trial with 52 provenances collected from Africa, South America and Asia in Tain II Forest Reserve in Central Ghana. This provenance trial was established to widen the genetic basis for teak establishment in West Africa. Using Genotyping by Sequencing (GBS) we analysed the genetic diversity of these provenances. Results of the study revealed that, although acquired from a wide geographical range, most teak provenances in the trial belong to only two distinct groups that are closely related. The implication of this finding is that, for breeding, a wider range of provenances is needed from the original teak distribution areas, and more specifically from Southern India. We conclude that urgent protection of older existing sources of genetic variation in teak, as well as an improvement of international collaboration under the Nagoya protocol with countries with native teak populations, is necessary.

Keywords: Teak, *Tectona grandis* L, provenance trial, Ghana, GBS

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Introduction

Teak is a high-quality timber species of great importance in plantation establishment throughout the tropics. Teak (*Tectona grandis* L.) is naturally distributed in Myanmar, India, Laos and Thailand (White, 1991) but can now be found in about 36 countries in Tropical Asia, South America and Africa (Koskela *et al*, 2014). A record area of about 5.7 million ha of teak has been planted (Bhat and Hwan, 2004; Nair, 2007), underlining the economic importance of teak for tropical forestry. Teak has reached such a large plantation area because it is easy to cultivate in a wide climatic amplitude (Orwa *et al*, 2009), grows fast and produces valuable timber. Growth rates of 15 to 20 m^3/ha/year are not uncommon on good sites. (Ugalde-Arias, 2013; Jerez and Coutinho, 2017) and the value of the timber can reach up to 800 USD/m^3 C/F (ITTO, 2020).

Except for the establishment of provenance trials in the 1970s, little effort seems to have gone into the improvement of genetic diversity in the countries where teak is widely planted. In fact, the trend seems to point to a narrowing of the genetic basis due to the wide use of the so called "Solomon Island Clones", which indeed provide superior growth and

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shape of the trees under many circumstances in various countries (Chaix *et al*, 2011; Goh and Monteuuis, 2012; Ugalde-Arias, 2013). Although such clones contribute to the present success and financial attractiveness of teak planting, tree planters should heed their genetic diversity. To help mitigate against the effects of climate change, the appearance of new diseases, and to allow for improvement of other qualities such as growth speed and heartwood formation, genetic diversity is key and should receive more attention (Graudal and Moestrup, 2017). It is important to initiate and support selection and testing of superior individuals in local breeding programmes because many traits such as bole straightness, proportion of heartwood and fine branching, which are important for commercial production of teak, have a genetic background (Kjær *et al*, 1996, 1999; Fofana *et al*, 2008), but the phenotypic manifestation of traits is not the same in each locality.

In Ghana, teak is the prime plantation species with well over 150,000 hectares planted since 2002 (FSD-FC Ghana, 2017). At present, for the development of teak plantations in Ghana, a very limited number of seed sources are available (Wanders, 2014; FSD-FC Ghana, 2017). Most of these seed sources are ‘unproven’, which means that the stands have been identified as seed stands, but progeny trials are not available to support the selection of these stands for this purpose. The material from these stands is now systematically evaluated at the Tain II Forest Reserve provenance trial at Form Ghana Ltd.

The stands that are currently used as seed sources were mostly planted in the 1980s and 1990s, many of them with material from Kihuhwi in Tanzania (FSD-FC Ghana, 2017). Other sources of planting material are what remains of an international teak provenance trialing effort containing 13 provenances from India, Laos, Indonesia and Ghana planted between 1972 and 1975 by the Danish Development Cooperation DANIDA and the Forest Research Institute of Ghana FORIG (Keiding *et al*, 1986). A clonal seed orchard has been developed based on material from this trial by FORIG at Jimira in Ghana. From these sources, plantation developers presently obtain seeds for plantation establishment. Some also resort to importation of seed from other countries.

Recognising the need for a wider genetic pool to source seeds, Form Ghana Ltd started a new provenance trial in 2015 in which, over several years, 52 accessions of teak coming from Ghana, Tanzania, Côte d’Ivoire, Malaysia, Brazil, Costa Rica, Honduras, and indirectly from India and Indonesia, were planted (Wanders, 2020).

While these provenances represent a global distribution of teak, there is great uncertainty on their genetic kinship. In this study, we investigated the genetic diversity of teak provenances presently grown for testing in Ghana. We evaluated how closely related the provenances are and whether the aim of a wider genetic base for the teak industry in West Africa can be achieved under the present conditions and with the material currently accessible.

Materials and methods

Trial location

The trial is located in block A42 in the Tain II Forest Reserve (Figure 1). The coordinates of the location are 7°37’53.78”N and 2°38’26.31”W. The layout of the trial is a block design with blocks of 49 trees per provenance. For most provenances there is at least one replicate, but some have several replicates. Planting started in 2015 and new material has been added annually, while also adding already present material to make comparisons within and between the years possible. In 2020 the trial covered 12 hectares.

Genetic sampling and sample library preparation

Leaf samples (one sample per provenance) were collected at Form Ghana’s Tain II provenance trial and at Form Ghana’s nursery in May 2019. Leaf samples were immediately dried with silica gel and stored for further processing. A total of 41 trees of 37 different accessions were sampled.

Genomic DNA extraction was done using a Nucleospin 96 Plant II Kit from Bioké, following the manufacturer’s instructions. Genetic variation was measured using Genotyping by Sequencing (GBS) (Elshire *et al*, 2011). First, 88 to 278 ng of genomic DNA (gDNA) of each of 41 samples was digested by two restriction enzymes (*AseI* and *NsiI*) after which, two indexed adapters were ligated to the DNA fragments. The main change in the adapter design was the incorporation of three random Unique Molecule Identifier (UMI) nucleotides per adapter for the identification of PCR duplicates within each amplified GBS library. After ligation, individual samples were cleaned by two subsequent Nucleo-Mag (Macherey-Nagel, Germany) clean-up steps of 1x and 0.8x beads. A small volume test PCR (15 cycles) was performed using KAPA HiFi HotStart readyMix (Roche Diagnostics, Switzerland). The resulting product was diluted 10,000 x prior to qPCR quantification (KAPA Library Quantification Kit for HTS, Roche Diagnostics, Switzerland). The result of the qPCR was subsequently used to equimolarly pool the original cleaned digestion/ligation products. This pooled product was concentrated using a column-based Nucleo-Mag PCR clean-up (Macherey-Nagel, Germany) and nick repaired using DNA polymerase I (50 μL reaction). The nick repaired product was amplified in five reactions of 10 μL each and cleaned by two subsequent NucleoMag (Macherey-Nagel, Germany) clean-up steps using 1x and 0.8x beads, respectively. The average library size was 1,177 bp. The final GBS library was quantified by qPCR, pooled with other libraries and spiked with 10% PhiX prior to sequencing. This increases the DNA complexity of the library in order to improve the Hiseq colour matrix estimation for which the first 11 sequencing cycles are

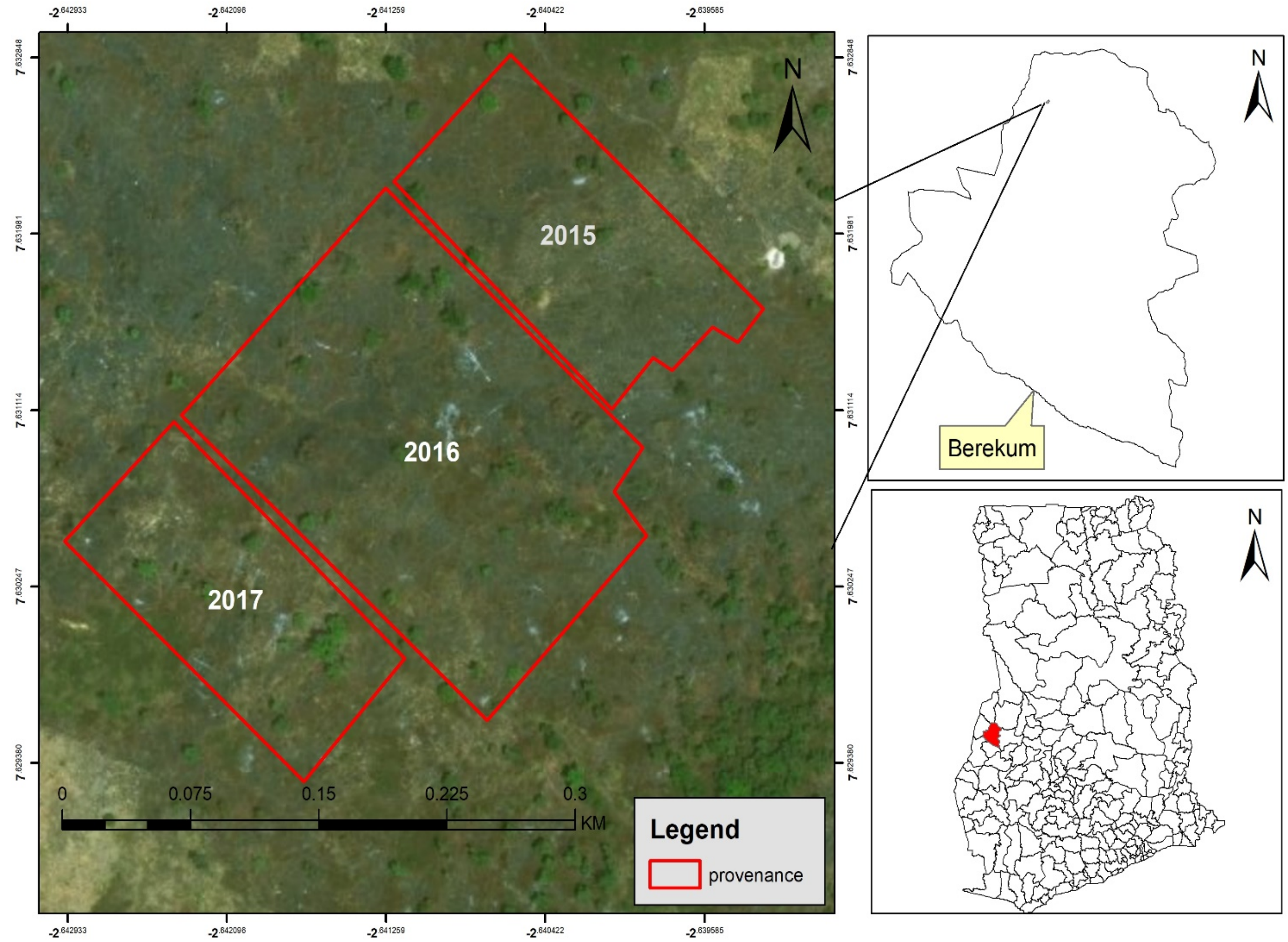

Figure 1. Map showing the location of the provenance trial in Ghana, and the various planting years sampled.

used overlapping with our index region. Sequencing was performed by Novogene (Hong Kong) on an Illumina Hiseq X-Ten sequencer, producing 2x150bp Paired-End (PE) sequencing reads. In total 0.4 sequence lane was devoted to the 41 teak GBS libraries, providing a total of 232,995,422 raw reads.

Data analysis

Demultiplexing, de novo reference construction, mapping and SNP calling of the DNA sequences were conducted using Stacks version 2.4 (Catchen *et al*, 2013). PCR duplicates were removed using clone filter based on the UMI nucleotides, followed by demultiplexing using process radtags. To identify SNPs from the reads we used the "denovo_map.pl" script using -m 3 -M 5 -n 5 based on exploratory runs using a range of values (-m 2-6, -M 3-7 and n=M) to maximise the quality of SNPs for this dataset (Paris *et al*, 2017). After mapping, data was filtered using VCF tools (Danecek *et al*, 2011). The applied filter first removed all loci which were not present in more than 50% of individuals, had a genotype quality below 30 or had a mean depth lower than six. After this, individuals with more than 80% missing data were removed. All SNPs, which were not present in all individuals and had an individual sample depth less than 10, were removed. Four duplicate datasets were removed from the analysis, resulting in a total of 37 samples. We used STRUCTURE (Pritchard *et al*, 2000) on 1000 randomly selected SNPs to assess patterns of genetic structure in the samples, with a number of assumed populations (K) of 1-7, with 10 replicates per K. We used 1,000,000 burn-in and 500,000 reps. Afterwards, the output data was analysed using structure selector (Li and Liu, 2018). Clustering was done using the Adgenet package (Jombart and Ahmed, 2011) in R version 3.5.3 (R Core Team, 2019). Genetic distance was calculated using the R-package Adegenet, using dist(method="Euclidian"). Principal component analysis was done with the function dudi.pca from the R-package Ade4. All scripts used in this analysis are available at https://github.com/MaartenPostuma/Teak-analysis. Demultiplexed reads are available under BioProject PRJNA756980 at NCBI (https://www.ncbi.nlm.nih.gov/bioproject/PRJNA756980).

Table 1. Analysed provenances, ID and their origin in this study.

Sample no.	ID / Provenance	Country	Country	Expected origin	Literature describing the source
1	Brazil 700	Brazil	Imported clones through Proteca	Solomon Islands	(Goh and Monteuuis, 2009; Monteuuis and Goh, 2015)
2	Brazil 701	Brazil	Imported clones through Proteca	Solomon Islands	
3	Bouaké (64)	Côte d'Ivoire	Bouaké	Côte d'Ivoire	(Wanders (2014)
4	Bamoro	Côte d'Ivoire	Bamoro seed stand SODEFOR	Côte d'Ivoire	(Dupuy and Verhaegen, 1993; Kadio, 2006; Kokou, 2010)
5	Bangsri Pati	Ghana	Danida provenance Trial in Nsoatre	Indonesia	(Keiding *et al*, 1986; Kjær *et al*, 1995)
6	Brazil T	Brazil	Mato Grosso	Brazil	
8	Catie	Costa Rica	278 Peñas Blancas	Costa Rica	
9	Dunkwa	Ghana	Oppon Mansi forest reserve	Tanzania	(Wanders, 2014)
10	Brazil F	Brazil	Mato Grosso	Brazil	
11	Goaso	Ghana	Bia Tano forest reserve	Tanzania	(Wanders, 2014)
12	Honduras	Honduras	La Cumbre seed stand	Honduras	
13	Jimira	Ghana	Jimira forest reserve	Mixed from Nsoatre PT in Ghana	(Wanders, 2014)
14	Kihuhwi p68	Tanzania	Provenance trial in Longuza	Tanzania	(Madoffe and Maghembe, 1988)
15	Kihuwi	Tanzania	Kihuhwi forest reserve	Tanzania	
16	Kiroka	Tanzania	Kiroka seed stand	Tanzania	
17	KVTC	Tanzania	Imported from KVTC seed stand	Tanzania	
18	La Téné	Côte d'Ivoire	La Téné seed stand, SODEFOR	Côte d'Ivoire (but based on PT, many provenances possible)	(Dupuy and Verhaegen, 1993; Kadio, 2006; Kokou, 2010)
19	Longuza	Tanzania	Imported from SFI	Tanzania	(Madoffe and Maghembe, 1988)
20	Luasong	Malaysia	Luasong, Tawau, Sabah	Malaysia	Goh and Monteuuis (2009); Monteuuis and Goh (2015)
21	Miro 1	Costa Rica	Catie 194/166- 25	Costa Rica	
22	Miro 2	Costa Rica	Catie 212/09B- 11	Costa Rica	
23	Miro 3	Costa Rica	Catie 221/45C- 12	Costa Rica	
24	Mtibwa p61	Tanzania	Provenance trial in Longuza	Tanzania	(Madoffe and Maghembe, 1988)
25	Mtibwa	Tanzania	Mtibwa seed stand	Tanzania	
26	Nigeria p67	Tanzania	Provenance trial in Longuza	Tanzania	

Continued on next page

Table 1 continued

Sample no.	ID / Provenance	Country	Country	Expected origin	Literature describing the source
27	Nilambur	Ghana	Danida provenance trial in Nsoatre	Kerala, India	(Keiding *et al*, 1986; Kjær *et al*, 1995)
28	North India	North India	North India	North India	
29	Oumé	Côte d'Ivoire	Oumé	Côte d'Ivoire	
30	Pampawie	Ghana	Pampawie Forest Reserve	Ghana	(Wanders, 2014)
31	Perlis	Malaysia	Perlis seed stand, Taliwas, Lahad Datu, Sabah	Malaysia	(Goh and Monteuuis, 2009; Monteuuis and Goh, 2015)
32	Sangoué	Côte d'Ivoire	Sangoué seed stand, SODEFOR	Côte d'Ivoire	(Dupuy and Verhaegen, 1993; Kadio, 2006; Kokou, 2010)
33	T1	Ghana	Danida provenance trial in Nsoatre	not traceable (likely Nilambur)	(Keiding *et al*, 1986; Kjær *et al*, 1995)
34	T4	Ghana	Danida provenance trial in Nsoatre	not traceable (likely Bangsri Pati)	(Keiding *et al*, 1986; Kjær *et al*, 1995)
35	Taliwas	Malaysia	Taliwas, Lahad Datu, Sabah	Malaysia	(Goh and Monteuuis, 2009; Chaix *et al*, 2011; Monteuuis and Goh, 2015)
36	Temandsang	Ghana	Danida provenance trial in Nsoatre	Indonesia	(Keiding *et al*, 1986; Kjær *et al*, 1995)
37	Topslip	Ghana	Provenance trial in Longuza	Coïmbatore, India	(Madoffe and Maghembe, 1988)
38	Worawora	Ghana	Wora Wora forest reserve	Ghana	(Wanders, 2014)

Results

A total of 23,182 SNPs were obtained after filtering, which ensured the accuracy and reliability of subsequent genetic diversity and population structure analyses. The optimal value of K was determined by Evanno's delta K method (Evanno *et al*, 2005). Two clearly defined main clusters (K=2; Figure 2) and a maximum of 4 clusters (K=4; Figure 2) were revealed. The most likely number of clusters was K=2. These two main clusters are at a great genetic distance from each other and are clustered primarily according to geographical region: one cluster consisted of teak stands originating from Asia and the Pacific and the other cluster originating from South America and Africa. In addition, K=3 and K=4 showed some variation within the two main clusters. When K=3, accessions originating from Côte d'Ivoire and Malaysia for example could be distinguished and at K=4 accessions from the Solomon Islands separated from the other accessions from the Asia-Pacific cluster. The list of provenances, ID and their collected and expected origin (as inferred from the genetic analysis) is shown in Table 1. 'Origin of collection' in this table means how Form Ghana obtained the material and the 'expected origin' in the table refers to the origin to which the material can be traced in the literature.

Further analysis of the two main clusters clearly showed more genetic similarities within the South America–Africa cluster indicating less genetic variability as compared to the Asia–Pacific cluster, which had less genetic similarities indicating more variation in genotype especially in the Asian cluster. This was also illustrated by a principal component analysis based on genetic distance (Figure 3) and the number of polymorphic sites (SNPs) within the two clusters. In the Asia–Pacific cluster, 94% of SNPs were polymorhpic compared to 74% of polymorphic SNPs in the South America–Africa cluster, even though the latter had more individuals. In addition, only 1364 private alleles were found in the South America–Africa cluster as compared to 6201 private alleles in the Asia–Pacific cluster. Mean Euclidean-based genetic distance was calculated as 87.25 ± 19.35 within the South America–Africa cluster (green + pink), 117.19 ± 43.9 within the Asia–Pacific cluster (yellow + red), and 161.35 ± 32.35 between these two main clusters (Figure 2). These data showed substantially higher levels of genetic variation in the Asia–Pacific cluster and suggest low levels of genetic variation in the South America–Africa cluster.

Discussion

The results in Figure 2 show two main clusters of genetic variation for the 37 teak provenances sampled in the Tain II Forest Reserve. The first cluster mainly consists of teak stands from Africa and South America and the second of provenances from Asia and the Pacific. Data on the number of polymorphic sites in the two clusters and genetic distance within and between the clusters indicate less genetic variation between provenances in the Africa-South America cluster and a high genetic variation between provenances within the Asia-Pacific cluster and especially in the Asia cluster.

Grouping the material shows that material from Indonesia and Africa is closely related which confirms the conclusions of Verhaegen *et al* (2010) that teak from Ghana and Indonesia could be originating from Laos while teak from other African places can be traced back to North India (Fofana *et al*, 2008). Together, they form a group that is different from the Thai and South India provenance groups. In this study we can now add the South American provenances to the latter group. The attribution of the Indonesian provenances to Laos was also found by Hansen *et al* (2017), who unfortunately did not sample from Ghana. The grouping of material from Malaysia and India in one group can be explained by the collection of Indian provenances in provenance trials in Côte d'Ivoire for the establishment of the Malaysian plots (Goh and Monteuuis, 2009). The link between the material from the Solomon Islands and India should not be surprising as the Solomon Islands have no indigenous teak population and their population was built up from foreign material which mostly came from India (Raomae, 2012).

Most teak provenances within the Africa-South America cluster showed less genetic variation in this study which confirms that African teak provenances most likely originate from a limited range in North India and none of the African provenances are from South India (Verhaegen *et al*, 2010).

Some uncertainty on the exact origin of provenances in our study remains. Attribution to a certain origin as indicated by the structure analysis was based on the genetic relatedness of samples from single trees representing each provenance. Based on this, provenances that were genetically more related were then assigned to the same cluster. However, some provenances originated from mixed clonal seed orchards (Jimira, Kiroka, Sangoué and La Téné) as presented in Table 1. The seed obtained from such seed orchards is potentially more diverse and sampling may have covered only part of the locally present diversity. As a consequence, more sampling in the same population of seedlings from such orchards could potentially also identify genetic material from the other cluster.

Despite the uncertainty of the origin of some provenances, the results show that although imports were made from very different areas in the tropics, the achieved gain in genetic diversity is very limited and reflects that, over time, teak provenances from a limited number of sources have spread over a wide area (Fofana *et al*, 2008). This also means that at present, new imports of teak seeds into e.g. Ghana, mostly do not constitute a new genetic accession added to the gene pool. Before going through the process of obtaining permits and importing seeds from a presumed new accession, it is important to compare its genetic makeup with the existing provenances. It is also important to further investigate the current collection of provenances

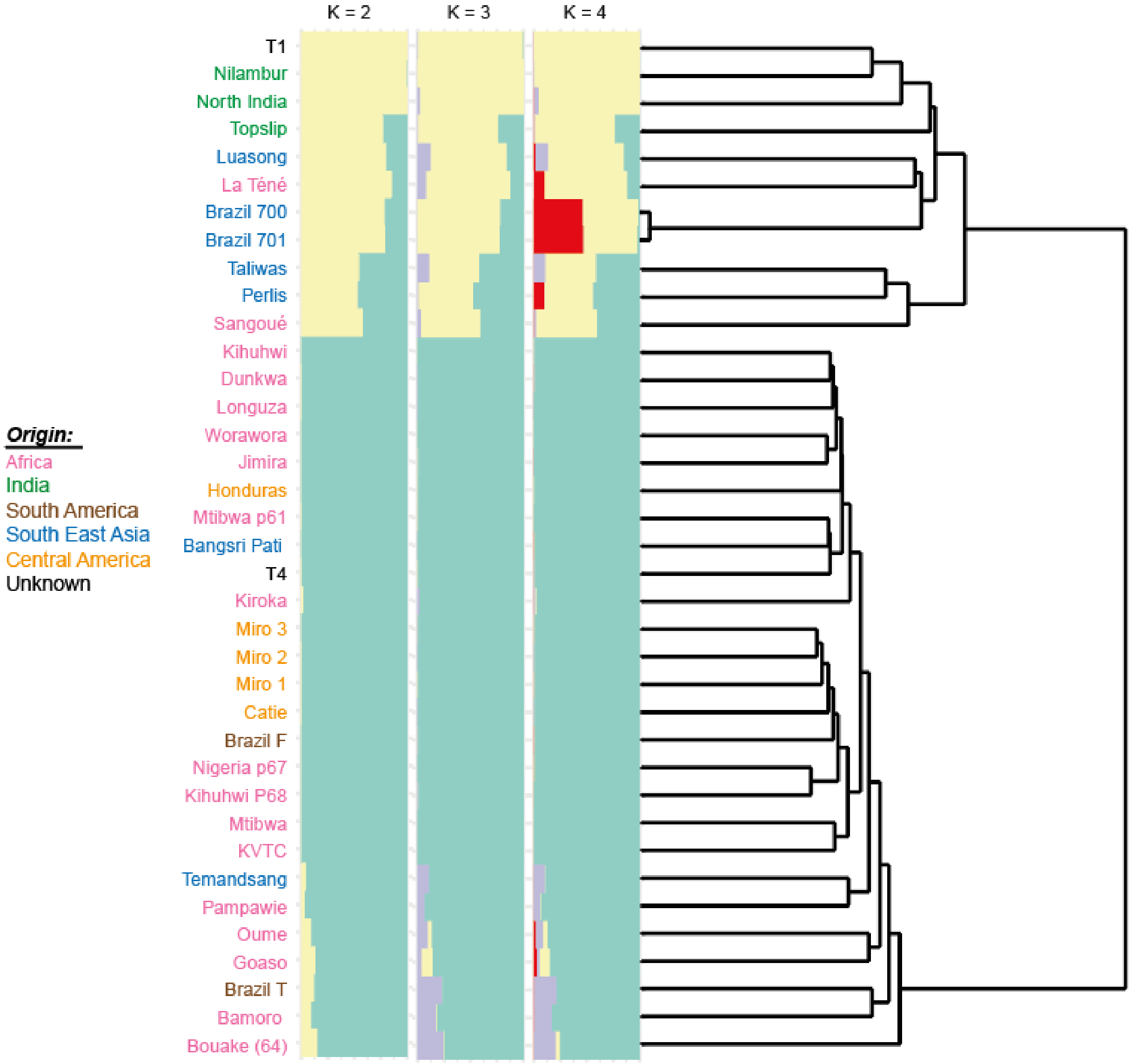

Figure 2. Clustering of teak stands of different provenances. Shown is a dendrogram based on genetic distance (right part) and the different clusters as identified by the structure analysis (green, cluster 1; yellow, cluster 2; pink, cluster 3 and red, cluster 4). The dendrogram was generated by hierarchical clustering (UPGMA) based on genetic dissimilarity. Vertical lines in the dendrogram give the amount of genetic dissimilarity and represent genetic lineages. Each row represents an individual tree per provenance, with the length of the different colour segments representing the proportion of a cluster in an individual's genetic makeup. K = 2–4 indicates the number of genetic clusters that were revealed in this structure analysis from 2 to 4. The most likely number of clusters was K=2.

so that the search for additional genetic material for teak provenance pools in West Africa can be conducted with more focus.

Our findings emphasise the need for acquiring teak provenances from areas of its original distribution that are high in genetic diversity and are not in the present provenance trial, one such area being South-West India (Hansen *et al*, 2017) and the semi-moist east coast of India (Hansen *et al*, 2015). The analysis of Vaishnav and Ansari (2018) indicates that genetic resources in India may be a source for screening resilient superior provenances for improvement strategies for sustainable production of quality timber on a large scale. Various examples exist for the benefit of matching specific provenances to specific local conditions. Indigenous teak populations from Annamalai Hills in the Indian states of Kerala and Tamil Nadu contain well performing provenances for Tanzania (Madoffe and Maghembe, 1988; Pedersen *et al*, 2007), while a Nilambur provenance from India and a Savannahket provenance from Laos have been assessed as very suitable for Ghana (Adu-Bredu *et al*, 2019).

Currently it is difficult to obtain accessions from some of the countries containing the high diversity areas, as they have banned the export of seeds and sometimes also of clones of their genetic heritage.

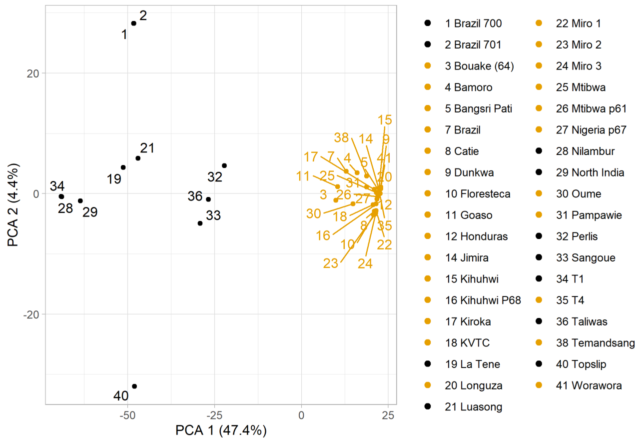

Figure 3. Principal components analysis on genetic distance of the different teak accessions. The different accessions are indicated by numbers, the two main clusters as identified by structure analysis by different colours.

It is, for instance, impossible to import seeds from India (Government Of India , 2002). This makes it all the more urgent to get a full view of the genetic make-up of trees planted in old (pre-Nagoya protocol) provenance trials such as the series of international provenance trials planted in the 1970s (Keiding *et al*, 1986). More and more of these trials are lost to felling, e.g. recently Longuza provenance trial in Tanzania (Wanders, personal observation) and to disaster as is the case of St. Croix in Puerto Rico, which was part of the series of international provenance trials set up by DANIDA and was destroyed by hurricanes (Morgan, personal communication, 2016). The original series of international provenance trials by DANIDA contained 75 provenances which were under test on over 50 locations, with 41 original teak provenances originating from the natural range of teak (Keiding *et al*, 1986). These trials potentially remain a very important source of genetic variety for any breeding programme (Koskela *et al*, 2014; Adu-Bredu *et al*, 2019) and their conservation should be a high priority. As the climate is changing and forestry is to adapt to the climate, becoming either wetter or drier, the need to access a wider range of genetic material may become more and more important in tropical forestry (Koskela *et al*, 2014).

At present, the Nagoya Protocol on access to genetic resources and benefit sharing (ABS) (CBD, 2011) could govern the sharing of benefits resulting from exchanges of genetic material in a more structured and mutually beneficial manner. It is not yet clear if the signing of the Nagoya protocol will make it possible to again obtain seeds from countries having interesting genetic resources, but prohibiting export of seeds and other propagation materials. Documents that need to be elaborated per seedlot, such as the Prior Informed Consent and benefit sharing agreement, create barriers that need urgent addressing at supranational level. Koskela *et al* (2014) provide an insight into the amount of paperwork necessary in order to plant a provenance trial, which is another argument to carefully conserve pre-Nagoya planted trials and exchange genetic material from these. The amount of work going into the drafting and signing of ABS and mutually agreed terms (MAT) may make it worthwhile to engage in only for commercially high returning crops.

In international forestry, non-profit initiatives to exchange seeds exist. One of these, CAMCORE (https://camcore.cnr.ncsu.edu/) has done excellent work on the collection and distribution of seeds for broad testing of Pinus and Eucalyptus species. CAMCORE has organised expeditions for the collection of seeds of species interesting for forestry and tree breeding and distributed these seeds to be planted in trials at member organisations and companies. CAMCORE has recently also started work on teak (Hodge *et al*, 2019). The cost of the membership fee for this organisation, however, is not accessible to all organisations involved in plantation development. More exchange would certainly improve the possibilities of increasing the gene pool for teak breeding.

Conclusion

As our work has shown, it can be difficult to have access to diverse genetic materials. With the uncertainties about the long-term fitness of currently available genetic material under climate change and possible disease vulnerability, having access to genetic diversity is becoming increasingly important. Because not all genetic diversity has a direct commercial interest, the creation and maintenance of a national gene bank or national collection (NCCPG, 2007; FAO, 2014) should be a national priority. Conservation of teak genetics in Thailand has been described by Kaosa-Ard *et al* (1998) and Graudal *et al* (1999). In India genebanks have also been created such as the National Teak Germplasm Bank in Chandrapur (Maharashtra) whose genetic diversity has been analysed (Mahesh *et al*, 2016). Lack of formal protection of tree genetic resources can cause genetic material to be lost unnoticed. Through cooperation between the countries that took part in past international provenance trials on teak, each participant country could, through exchanges, build up a collection of most, if not all, accessions of teak originally distributed. This should be done in addition to addressing of international barriers for exchange of genetic material of teak from its original range mentioned earlier. A national teak genebank collection for Ghana (and other African teak producing countries) would then become an excellent centre for the distribution and conservation of genetic material. The facility managing such a collection should become a member of CAMCORE or a similar organisation to further facilitate exchange.

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Author contributions

Tieme Wanders, Philippine Vergeer, James Ofori and Elmar Veenendaal conceived and planned the experiments; James Ofori, Alexander Amoako and Tieme Wanders collected data; Philippine Vergeer, Niels Wagemaker, Maarten Postuma, James Ofori, Tieme Wanders and Elmars Veenendaal contributed to analysis and interpretation of the results; Tieme Wanders took the lead in writing the manuscript. All authors provided critical feedback and helped shape the research, analysis and manuscript.

Conflict of interest statement

The authors declare no conflicts of interest.

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West African Crop Wild Relative Checklist, Prioritization and Inventory

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Abstract: Crop wild relatives (CWR) are wild plant taxa genetically related to domesticated crops with trait diversity that can be used in plant breeding to sustain food security. Prioritization is a prerequisite for the cost–effective conservation of CWR as it allows CWR in a checklist to be reduced to a manageable number for active conservation action. In this study, a partial CWR checklist comprising 1651 taxa was compiled for West Africa. Prioritization of the annotated CWR checklist was based on three criteria: (i) economic value of the related crop in West Africa, (ii) CWR genetic closeness to its related crop and (iii) threat status. After applying the three criteria using the parallel method of prioritization, 102 priority CWR were selected for active conservation action. The priority CWR are related to food crops that are nationally, regionally and globally important, such as white guinea yam (*Dioscorea cayenensis* subsp. rotundata (Poir) J. Miège), cassava (*Manihot esculenta* Crantz), rice (*Oryza sativa* L.), wheat (*Triticum aestivum* L.), cowpea (*Vigna unguiculata* (L.) Walp.), sweet potato (*Ipomea batatas* (L.) Lam.), common bean (*Phaseolus vulgaris* L.) and sorghum (*Sorghum bicolor* (L.) Moench). This CWR checklist and prioritization will help in the development of a regional conservation action plan for West Africa.

Keywords: Crop wild relative, checklist, prioritization, inventory, crop improvement, conservation

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Introduction

The significant effects of climate change on agriculture and livelihood in West Africa recently show the need to develop varieties of crops that can adapt to the rising temperatures, desertification, unpredictable rainfalls, floods and droughts and new diseases and pests, as well as meet the yield quality and quantity requirements of producers and consumers (Maxted *et al*, 2015; Mousavi-Derazmahalleh *et al*, 2018; Allen *et al*, 2019). Climate change has led to yield losses in different crops and will continue to adversely affect agriculture with considerable yield decline predicted in West Africa (Sultan *et al*, 2019). IPCC reported that the duration of the growing season in West Africa may be reduced by 20% in 2050, resulting in about 40% yield reduction in cereals (Zougmoré *et al*, 2016). The increasing population in the Western Africa region may further limit the ability of the region to meet the food and nutrient security needs of its growing population. CWR are wild plant taxa genetically related to domesticated crops and are widely recognised as a major reservoir of valuable diversity that can be used in plant breeding to sustain food and nutrient security in the future (Maxted *et al*, 2006; Magos Brehm *et al*, 2017; Herden *et al*, 2020; Kioukis *et al*, 2020). Many CWR thrive in marginal environments (Jarvis *et al*, 2015; Phillips *et al*, 2017; Vincent *et al*, 2019), making them better suited to withstand changing climate conditions. The extensive genetic diversity in CWR has been used globally in plant breeding programmes to produce crop cultivars with traits for high yield, drought tolerance, disease resistance, good handling quality, seed

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weight, early flowering time, cooking quality and better storage quality (Maxted and Kell, 2009; USDA, 2011).

CWR conservation and use contributes to the Sustainable Development Goal (SDG) of the United Nations (United Nations, 2015). Also, the United Nations' Intergovernmental Science – Policy Platform on Biodiversity and Ecosystem Service (IPBES), described CWR as vital for future food and nutrient security, ameliorating ecosystems and adapting crops to marginal environments (IPBES, 2019).

There are about 45,000 plant species in Sub-Saharan Africa (Linder, 2014). In Nigeria alone, there are thought to be 7,895 different plant species (Federal Republic of Nigeria, 2010). However, the diversity of CWR is widely threatened by unsustainable use of natural resources, urbanization, deteriorating environmental conditions, the introduction of exotic species and climate change (Maxted and Kell, 2009; Magos Brehm *et al*, 2017). Several CWR thrive on farmlands and are therefore threatened by agrochemical inputs and intensive agricultural systems (Jarvis *et al*, 2015; Capistrano-Gossmann *et al*, 2017; Vincent *et al*, 2019). Also, increasing population, poverty, habitat destruction, overgrazing, lack of land use planning and deforestation causes biodiversity loss in West Africa (Adejuwon, 2000). There is therefore the need for active *in situ* and *ex situ* conservation of CWR in West Africa, to ensure they continue to provide profitable genes to produce plant cultivars to meet the growing demand for ample food supply for the people of West Africa and beyond.

Developing a regional and national conservation plan is essential if poverty alleviation and food provision is to be maximised. This starts with making an inventory of CWR. Several countries already have CWR inventory, such as UK (Fielder *et al*, 2012), USA (Khoury *et al*, 2013), China (Kell *et al*, 2015) and Indonesia (Rahman *et al*, 2019). A CWR checklist is a list of CWR taxa found in a defined geographical area. A CWR checklist may contain additional information on the priority CWR which are important for conservation planning including taxon distribution, reproduction and conservation status, turning the checklist into a CWR inventory. As reported by Magos Brehm *et al* (2017) the steps involved in the generation of a CWR inventory are: (i) compilation of a national flora, (ii) matching the national flora against an existing digitized list of crop genera to obtain a list of taxa of the same genera as the list in the national flora, thereby producing the CWR checklist, (iii) prioritization of the CWR checklist to generate a realistic and manageable number of priority CWR, and (iv) annotation of the priority list of CWR with additional information for active conservation action to produce a CWR inventory (Maxted *et al*, 2007; Magos Brehm *et al*, 2017). Prioritization involves reducing the number of taxa in the CWR checklist into a number manageable for active conservation actions due to resource constraints and funding limitations. The prioritization criteria may include crop socio-economic value, CWR genetic closeness and ability to donate genes to the related crop, endemicity, occurrence, threat status and other related parameters (Magos Brehm *et al*, 2017; Thormann *et al*, 2017). There is presently no complete CWR checklist or inventory for West Africa.

This paper aims at the generation of a regional CWR checklist for West Africa, prioritization of this CWR checklist and the compilation of a CWR inventory, using the method described by Maxted *et al* (2007).

Materials and Methods

Creation of a CWR checklist for West Africa

A monographic approach (for selected crop genera) was carried out in order to produce a digitized CWR checklist (Magos Brehm *et al*, 2017) for West Africa, including the following countries: Benin, Burkina Faso, Cape Verde, Cote d' Ivoire, Gambia, Ghana, Guinea, Guinea- Bissau, Liberia, Mali, Mauritania, Niger, Nigeria, Senegal, Sierra Leone and Togo. A digitized flora for families known to contain CWR taxa was compiled for 12 selected plant families. WCSP (2020) was used for the *Araceae, Arecaceae, Convolvulaceae, Dioscoraceae, Euphorbiaceae, Musaceae, Poaceae* and *Zingiberaceae*, while the regional printed flora (Huchinson and Dalziel, 1958) was used for the *Malvaceae, Papilionaceae, Sterculiaceae* and *Caricaceae*.

The following steps were involved in generating the CWR checklist:

(i) Produce a digitized list of regional flora:

All taxa (i.e. species, subspecies, and varieties) belonging to the selected plant families were included in the floristic checklist. Information related to the different taxa of the regional flora was entered in the CWR checklist and inventory data template v.1 (Thormann *et al*, 2017), including: family, genus, species and authorities, various sub-ranks, taxon, subtaxon, taxon common name, synonyms, related crop(s) and common name of the related crop (Thormann *et al*, 2017; Rahman *et al*, 2019).

(ii) Produce a digitized list of crops:

A digitized list of crop genera was produced from the following sources: (i) all crops cultivated in the world (FAO, 2021), (ii) major and minor food crops from the World Atlas of Biodiversity (Groombridge *et al*, 2002), and (iii) Annex 1 of the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA) for both forage and food crops (FAO, 2009). The digitized list of crop genera was obtained from a published crop and crop genus list for CWR checklist and prioritization (Kell, 2016).

(iii) Match the crop genera against the floristic checklist to produce the CWR checklist:

The digitized list of crops was matched against the floristic list to produce the CWR checklist (Magos Brehm *et al*, 2017). Taxa cultivated but with no wild relatives in West Africa such as cocoyam (*Colocasia esculenta* (L.) Schott), coconut (*Cocos nucifera* L.), oil palm (*Elaeis guineensis* Jacq) or maize (*Zea mays* L.) were removed. The draft CWR checklist was sent to experts and agricultural stakeholders for validation. The draft CWR checklist was approved by the experts and agricultural stakeholders for prioritization.

CWR Prioritization

Different criteria and methods have been used to prioritize CWR checklists in the past for several countries and regions of the world, depending on the country and who will fund the CWR conservation action (Magos Brehm *et al*, 2017). In this work, three criteria were applied in the prioritization of the CWR checklist for West Africa (Maxted *et al*, 2013): (i) crop value in West Africa from FAOSTAT, (ii) CWR closeness to the crop from the Harlan and de Wet CWR diversity (https://www.cwrdiversity.org/checklist/) and (https://npgsweb.ars-grin.gov/gringlobal/taxon/taxonomysearchcwr.aspx), with CWR closeness restricted to gene pool or proven use in breeding within tertiary gene pool (GP3) (Maxted and Kell (2009), and (iii) global threat status according to IUCN (https://www.iucn.org/).

A parallel method was used through a point scoring process in which taxa were scored for all criteria, ranked according to their total score, and selected based on a 'cut off' score. For all criteria, taxa with a score of ≥3 were selected for prioritization. In assigning scores to criterion one (value), human food crops were scored (7 points), crops used as food additive (5), material (3), animal feed (1) and environmental use (1). Food crops (important for nutrition and food security), food additives and materials were selected for prioritization, excluding animal feed and environmental use crops. In assigning scores to the second criterion (genetic closeness), GP1 was scored (9 points), GP2 (7), GP3 (3), and CWR that lack this information [i.e. those belonging to Taxon Group 4 (TG4)] were scored (1 point). TG4 are CWR that belong to the same genus with their related crop. Applying the second criterion, CWR belonging to the primary gene pool (GP1B), secondary gene pool (GP2), and tertiary gene pool (GP3) with proven use in crop improvement were selected for prioritization (Ford-Lloyd *et al*, 2008). Based on the third criterion (threat status), all evaluated CWR were selected for prioritization, excluding CWR that have not been evaluated (Maxted *et al*, 2013).

Results

The monographic CWR checklist for West Africa contains 1651 taxa from 379 genera. After the digitized list of crop genera was matched with the floristic list, a total of 392 CWR (and crops) resulted, belonging to 46 genera. Cultivated taxa without wild relatives in West Africa were removed, bringing the number to 379 taxa belonging to 33 genera. After applying the three criteria of the parallel method for prioritization (Kell *et al*, 2017; Ng'uni *et al*, 2019), the CWR checklist was reduced to a total of 102 priority CWR from 18 genera with 24 sub-taxon (subspecies/varieties). The priority CWR are related to 15 crops or crop groups important for the West African region. The families with the highest number of CWR species are *Poaceae* (39), *Papilionaceae* (26), *Dioscoreaceae* (15) and *Convolvulaceae* (13). The genus with the highest number of CWR are *Vigna* (23), *Dioscorea* (15), *Ipomoea* (13), *Oryza* (6) and *Cola* (5) (Table 1).

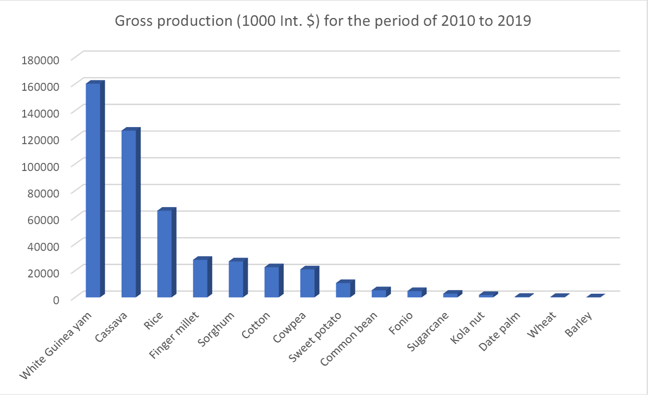

Figure 1. Gross Production Value for the period 2010-2019 of socio-economically valuable crops in West Africa. Data source: FAO (2021).

Socio-economic Value of Related Crops

Yam (*Dioscorea cayenensis* subsp. *rotundata* (Poir) J. Miege) is the most economically valuable crop in West Africa, with the highest gross production value (Supplemental Table S3). It is followed by cassava (*Manihot esculenta* Crantz), rice (*Oryza sativa* L.), finger millet (*Eleusine coracana* (L.) Gaertn), sorghum (*Sorghum bicolor* (L.) Moench), cotton (*Gossypium hirsutum* L.) and cowpea (*Vigna unguiculata* (L.) Walp.) (Figure 1). Yam (*Dioscorea cayenensis* subsp. *rotundata* (Poir) J. Miège) also has the second largest number of CWR (15) after cowpea (23). Cassava (*Manihot esculenta* Crantz) and rice (*Oryza sativa* L.) which are the second and third in gross production value, have five and six CWR, respectively in the inventory (Table 1).

CWR Closeness to Related Crops

Forty-five 45 (44 %) of the taxa were selected for prioritization using the criterion of taxa belonging to gene pools GP1B, GP2 or proven use of GP3 in crop improvement. Among the CWR selected, 21 (20.58 %) belong to GP1B, 28 (27.4%) are GP2 while 53 (51.9%) belong to GP3 or Taxon Group 4 (Supplemental Table S1). Among the 53 CWR belonging to GP3/Taxon Group 4, three (2.9%) have potential and confirmed use in crop improvement. Twenty-two (21.7%) of the CWR have confirmed use in crop improvement for crops such as wheat, rice, yam, sorghum, cassava, cowpea, millet and cotton, contributing to yield improvement, drought tolerance and resistance to several diseases in different crops as well as fibre quality in cotton (Table 2). Out of the 14 CWR taxa in the genus Dioscorea, five have confirmed use in crop improvement against various diseases such as anthracnose, yam mosaic virus (YMV) and yam nematode. Four CWR out of six

Table 1. Numbers of priority CWR for West Africa and their related crops.

Family	Genus	Related crop	No. of CWR taxa
Areceae	*Phoenix*	Date palm	1
Convolvulaceae	*Ipomoea*	Sweet potato	13
Dioscoreaceae	*Dioscorea*	White yam	15
Euphorbiaceae	*Manihot*	Cassava	5
Malvaceae	*Gossypium*	Cotton	3
Papilionaceae	*Phaseolus*	Common bean, kidney bean	3
	Vigna	Cowpea	23
Poaceae	*Digitaria*	Fonio	4
	Eleusine	Finger millet	3
	Eragrostis	Teff	4
	Hordeum	Barley	2
	Oryza	Rice	6
	Saccharum	Sugarcane	2
	Sorghum	Sorghum	4
	Triticum	Wheat	2
	Echinochloa	Barnyard millet, Japanese millet	5
	Panicum	Proso millet	2
Sterculiaceae	*Cola*	Kola nut	5
		Total CWR	102

in the genus Manihot have confirmed utilization for crop improvement against cassava brown streak disease (CBSD).

Threat Status of CWR

The threat status of 71 (69.6%) of the priority CWR has been determined under the IUCN threat assessment criteria (IUCN, 2012). All the priority CWR were globally assessed. *Vigna desmodioides* R. Wilczek is the only Endangered (EN) priority CWR. Two priority CWR are Near Threatened (NT): *Dioscorea sensibarensis* Pax and *Gossypium anomalum* Wawra. Two CWR are Data Deficient (DD): *Gossypium herbaceum* var *acertifolium* (Guill & Perr.) A. Chev. and *Oryza brachyantha* A. Chev. & Roehr. Sixty-six (64.7%) of the priority CWR are Least concern (LC) while 31 (30.4%) were Not Evaluated (NE) (Figure 2). Rice (*Oryza sativa* L.) was the only socio-economically valuable crop that had all its CWR assessed for threat status (Huchinson and Dalziel, 1958).

CWR Distribution

Eighty-four (69%) of the priority taxa were regionally endemic to West Africa, and 10 (8%) were nationally endemic. The nationally endemic priority taxa included: *Oryza eichingeri* Peter and *Cola attiensis* Aubrév. & Pellegr. (Cote D' Ivoire), *Cola angustifolia* K.Schum. (Sierra Leone), *Ipomoea intrapilosa* Rose, *Ipomoea prismatosyphon* Welw., *Vigna ambacensis* Welw. ex Bak., *Vigna macrorhyncha* (Harms) Milne–Redh., *Cola altissima* Engl. and *Cola argentea* Mast. (Nigeria) (Huchinson and Dalziel, 1958) (Supplemental Table S2). Six priority taxa (5%) were found in all 15 countries in West Africa and include: *Echinochloa colona* (L.) Link, *Echinochloa pyramidalis* (Lam.) Hitchc. & Chase, *Eragrostis japonica* (Thunb.) Trin., *Eragrostis pilosa* (L.) P.Beauv., *Oryza barthi* A. Chev. and *Eleusine indica* (L.) Gaertn. (Huchinson and Dalziel, 1958; WCSP, 2020) (Supplemental Table S2).

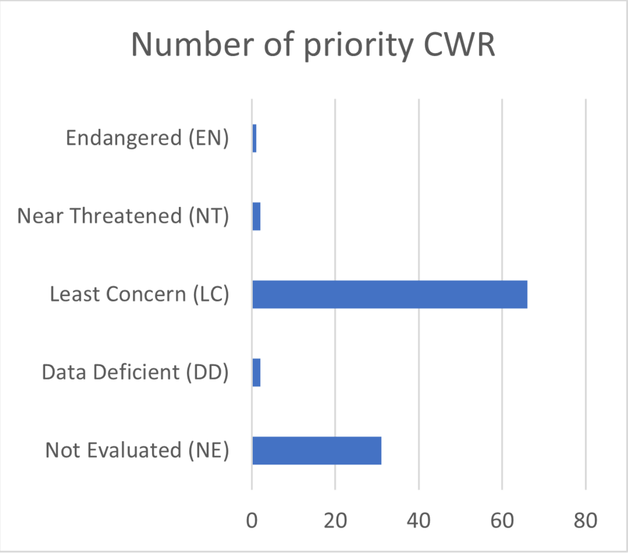

Figure 2. Number of priority taxa in the IUCN categories. Data source: IUCN (2020).

Table 2. Confirmed and potential use of priority CWR for Nigeria and West Africa in crop improvement.

Crop	CWR	Confirmed and potential use
White Guinea yam	*Dioscorea abyssinica* Hochst. ex Kunth	Yam mosaic virus (YMV) and anthracnose resistance (Lopez-Montes *et al*, 2012)
	Dioscorea praehensilis Benth.	Yam mosaic virus (YMV) and anthracnose resistance (Lopez-Montes *et al*, 2012)
	Dioscorea alata L.	Anthracnose resistance, improved cooking quality and reduced tuber oxidation (Lopez-Montes *et al*, 2012)
	Dioscorea bulbifera L.	Yield improvement (Saini *et al*, 2016)
	Dioscorea cayennensis Lam	Anthracnose and yam nematode resistance, drought tolerance (Lopez-Montes *et al*, 2012)
Cassava	*Manihot esculenta* subsp. *peruviana* Crantz	Cassava brown streak disease (CBSD) resistance (Kawuki *et al*, 2016)
	Manihot carthagenensis subsp. *glaziovii* (Müll. Arg.) Allem *Manihot dichotoma* Ule *Manihot esculenta* subsp. *flabellifolia* Crantz	
Cotton	*Gossypium barbadense* L.	High fibre quality (Zamir, 2001; Shi *et al*, 2008)
Barnyard millet, Japanese millet	*Echinochloa crus-galli* (L.) P. Beauv. *Echinochloa frumentacea* Link	High yield (Sood *et al*, 2015)
Finger millet	*Eleusine africana* Kenn.-O' Byrne	High yield (Dida and Devos, 2006)
Barley	*Hordeum bulbosum* L.	Barley mild mosaic virus resistance (Walther *et al*, 2000; Ruge *et al*, 2003; Wendler *et al*, 2015); barley yellow dwarf virus resistance (Scholz *et al*, 2009; Wendler *et al*, 2015) barley yellow mosaic virus resistance (Ruge-Wehling *et al*, 2006);leaf rust resistance (Shtaya *et al*, 2007; Johnston *et al*, 2013; Park *et al*, 2015); leaf scald resistance (Pickering *et al*, 2006); powdery mildew resistance (Pickering and Johnston, 2005; Johnston *et al*, 2009); stem rust resistance (Fetch-Jr *et al*, 2009); potential use for soil salinity tolerance (Tavili and Biniaz, 2009); potential use for high yield (Kakeda *et al*, 2008)
Rice	*Oryza eichingeri* Peter	Potential use for brown planthopper resistance, green leafhopper resistance and white backed planthopper resistance (Jena, 2010), submergence tolerance (Atwell *et al*, 2014)
	Oryza barthii A.Chev.	Potential use for drought tolerance (Atwell *et al*, 2014)
	Oryza glaberrima Steud.	rapid leaf canopy establishment (Jones *et al*, 1997); drought tolerance (Hajjar and Hodgkin, 2007); iron tolerance, potential for acid soil tolerance (Brar, 2004); potential for heat tolerance (Atwell *et al*, 2014)
	Oryza longistaminata A. Chev. & Roehr.	Drought tolerance (Hajjar and Hodgkin, 2007); yield improvement (Brar, 2004); bacterial blight resistance (Brar, 2004; Jena, 2010)

Continued on next page

Table 2 continued

Crop	CWR	Confirmed and potential use
	Oryza punctata Kotschy ex Steud.	Potential use for drought resistance (Atwell *et al*, 2014); brown planthopper resistance and zigzag leafhopper resistance (Jena, 2010)
Sorghum	*Sorghum purpureosericeum* (Hochst. ex A. Rich.) Schweinf. & Asch.	Sorghum shoot fly resistance (Nwanze *et al*, 1990)
	Sorghum bicolor subsp. *verticilliflorum* (L.) Moench	Leaf rust resistance (Park *et al*, 2015); spot blotch resistance (Yun *et al*, 2006); stem rust resistance (Fetch-Jr *et al*, 2009); drought tolerance (Nevo and Chen, 2010); seed weight (Pillen *et al*, 2004)
Common bean, kidney bean	*Phaseolus vulgaris* var *aborigineus* (Burkart) Baude	Drought tolerance (Blair *et al*, 2016); plant height, seed size (Blair *et al*, 2006); yield improvement (Wright and Kelly, 2011); bruchid resistance (Osborn *et al*, 2003); common bacterial blight resistance, web blight resistance (Beaver *et al*, 2012); white mold resistance (Mkwaila *et al*, 2011); potential for bean rust resistance (Acevedo *et al*, 2006); potential for fusarium root rot resistance (de Ron *et al*, 2015)
Cowpea	*Vigna unguiculata* subsp. *dekindtiana* (Harms) Verdc.	Pod bug resistance (Timko and Singh, 2008)
	Vigna unguiculata var. *spontanea* (Schweinf.) Pasquet	Yield improvement (Andargie *et al*, 2014)
	Vigna unguiculata subsp. *stenophylla* (Harv.) Marechal & al.	Potential for aphid resistance (Badiane *et al*, 2014)
Wheat	*Triticum turgidum* L.	Stripe rust resistance, powdery mildew resistance (Chaudhary *et al*, 2014)

Discussion

Adejuwon (2000) reported that 20 species of plants in Nigeria were extinct, 431 were endangered species while 20 were vulnerable. Urbanization, soil degradation, natural calamities, deforestation, forest fires, overgrazing and other anthropogenic activities, particularly climate change, are reducing the availability of CWR for sustainable agricultural productivity (Maxted *et al*, 1997; Moore *et al*, 2008; Mounce *et al*, 2017). For an effective and sustainable regional conservation strategy and its subsequent implementation, a priority CWR inventory is essential. A CWR inventory serves as a guide for a sustainable conservation action plan. The outcome of this research will form the blueprint for a systematic conservation and use strategy for West Africa. It will provide a starting point for a coordinated policy in the conservation and sustainable utilization of CWR diversity in the West African region. In this study, 379 taxa were identified as priority plant taxa, of which 122 were subsequently prioritized for urgent active conservation action. The remaining 257 plant species and their CWR could be considered for active conservation in the future as and when resources become available.

CWR of socio-economic valuable crops in West Africa have been reportedly used in crop improvement. For instance, Sood *et al* (2015) reported the use of *E. crusgalli* (P. Beauv) and *E. frumentacea* (Link) to increase yield quality in Barnyard millet. *D. abysinica* (Hochst ex Kunth) and *D. praehensilis* have been reported to show resistance to yam mosaic virus and anthracnose , while *D. bulbifera* showed resistance to yam nematode and tolerance to drought (Lopez-Montes *et al*, 2012). Similarly, Kawuki *et al* (2016) reported the use of *M. esculenta* subsp. *peruviana* Crantz, M. *carthagenensis* subsp. *glaziovii* (Müll. Arg.) Allem, *M. dichotoma* Ule and *M. esculenta* subsp. *flabellifolia* Crantz in breeding against cassava brown streak disease in cassava (Table 2). Traits for drought tolerance (Hajjar and Hodgkin, 2007), yield improvement (Brar, 2004) and bacterial blight resistance (Brar, 2004; Jena, 2010) have been transferred from *O. longistaminata* A. Chev. & Roehr. to rice, while *O. glaberrima* Steud. has been reported to show drought tolerance (IRRI, 2006), iron tolerance (Brar and Khush, 2002), rapid leaf canopy establishment (Jones *et al*, 1997) and potential for tolerance to acid soil (Brar and Khush, 2002) and heat (Atwell *et al*, 2014). Also, *S. bicolor* subsp. *verticillifolia* (L.) Moench has reportedly shown resistance to leaf rust (Park *et al*, 2015), spot blotch (Yun *et al*, 2006), stem rust (Fetch Jr *et al*, 2009) and tolerance to drought (Nevo and Chen, 2010). Resistance to white mold (Mkwaila *et al*, 2011), bruchids (Osborn *et al*, 2003), common bacterial blight and web blight (Beaver *et al*, 2012), and tolerance to drought have been documented in *Phaseolus vulgaris* var, *aborigineus* L. Chaudhary *et al* (2014) reported stripe rust and powdery mildew resistance in *T. turgidum* L. (Table 2).

Maxted *et al* (2015) and Kell *et al* (2017) have opined that regional conservation is supplemental to national efforts as some CWR may be lacking in some countries in a region. West Africa, being a region dominated by agricultural nations, will find the implementation of the conservation plan from this inventory useful, as it will enhance the region's global relevance in agricultural productivity. As reported by Maxted *et al* (2008) and Engels and Thormann (2020), collaboration by neighboring nations could enhance the extensive and effective conservation of CWR genetic diversity. It is therefore the collective responsibilities of the neighboring nations where this CWR diversity is found to regionally conserve it (Maxted *et al*, 2008, 2015; Kell *et al*, 2017; Allen *et al*, 2019).

Conclusion

This study shows that West Africa harbours CWR diversity that can contribute significantly to sustainable agricultural development in the region. Kell *et al* (2015) noted that countries should widen their utilization of CWR across national boundaries and all nations are inter-independent in the quest for food security. Similar to an existing CWR inventory for the North African region (Lala *et al*, 2018), the CWR checklist, prioritization and prioritized inventory presented in the study will help in the development of a CWR conservation plan for West Africa. The conservation and utilization of CWR in this inventory for crop improvement has the potential to significantly reduce the over-dependence on synthetic agrochemicals and fertilizers in the region, which negatively impacts on its biodiversity and agricultural productivity. There is an urgent need to take a systematic and pragmatic approach in the conservation and sustainable utilization of CWR diversity in West Africa to ensure food security.

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Supplemental data

Supplemental Table 1**:** Related crop and concept level of priority CWR for West Africa.

Supplemental Table 2**:** Endemicity and International Union for Conservation of Nature and Natural Resources (IUCN) category of priority CWR.

Supplemental Table 3**:** Gross production value of socioeconomically valuable crops in West Africa.

Author contributions

Nigel Maxted and Joana Magos Brehm designed the study. All authors were involved in checklist compilation and prioritization. Michael Nduche wrote the manuscript while all authors discussed the results, commented on the manuscript, read and approved the final manuscript.

Conflict of interest statement

The authors declared that there is no conflict of interest.

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Estimation of genetic erosion on Ethiopian tetraploid wheat landraces using different approaches

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Abstract: The demand and use of improved crop varieties by farmers has increased in the central highlands of Ethiopia, where continuous loss of local traditional varieties has been occurring in the last two to three decades. The objectives of the study were to assess the extent of genetic erosion and perception of farmers and associated causes for the reduction of traditional farmers' varieties. Direct field assessment covering 56 wheat farms and a survey in which 149 farmers participated were carried out in three districts of central Ethiopia. Based on data collected during direct farm assessment, the loss of genotypes was found to be 88% in Ada followed by 80% and 60% in Lume and Gimbichu districts, respectively. The farmer survey indicated an even greater loss of diversity of100% in Ada followed by Lume (93%) and Gimbichu (67%). Diseases and pests as well as shorter growing seasons associated with climate change were identified as main causes for farmers to switch to modern varieties. The expansion of high yielding improved bread and durum wheat varieties also contributed to gradually replace local durum wheat varieties by local farmers of these districts. Overall, genetic erosion of tetraploid wheat varied among the three districts of central Ethiopia. Reductions in the number of farmers and area coverage in the study districts could be used as good indicators for the existence of genetic erosion.

Keywords: Direct farm assessment, Genetic erosion indicators, Genetic integrity, Landraces, Tetraploid wheat

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Introduction

Ethiopia is the largest wheat producer in Sub-Saharan Africa with about 1.6 million ha of durum and bread wheat (Central Statistical Agency, 2017). Wheat is one of the major cereal crops in the Ethiopian highlands, which range between 6 and 16 N latitude, 35 and 42 E longitudes, and from 1500 m to 2800 m above sea level (masl). Ethiopia has already been identified as an important center of diversity for different crops. Durum wheat is a tetraploid wheat variety traditionally grown on heavy black clay soils (Vertisols) of the Ethiopian highlands between 1800-2700 masl, where it is mainly produced by small scale farmers. Durum wheat is suitable for manufacturing pasta products (e.g. macaroni, spaghetti); however, in Ethiopia it is also used for making "injera", a white leavened Ethiopian bread made from grain flour, and other local foods. Durum wheat grown in Ethiopia is constituted by a few improved varieties and a large number of traditional farmers varieties, commonly referred to as landraces (Bechere *et al*, 2000; Eticha *et al*, 2006; Bishaw *et al*, 2014).Durum wheat is extensively cultivated and grown by a large number of farmers and a significant number of traditional farmers' varieties have been recorded in the central highlands of Ethiopia in the past 20 to 30 years (Negatu *et al*, 1992). Statistics on durum wheat production in Ethiopia from the past decades are difficult to obtain, they are usually lumped with bread wheat in reporting. The total area under wheat production in 1983was reported to be 625,590 ha of which 60-70% was estimated to be used forthe production of durum (Tesema, 1991). The following

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decades saw a drastic reduction in area coverage for durum wheat which dropped to around 50% of total wheat production area (Gashawbeza *et al*, 2003). Recent reports indicated that the area coverage for durum has further declined to not more than 15-20% from a total 1.6 million ha of lands (Mengistu *et al*, 2016).

Introduction of modern varieties, improved production practices and problems associated with biotic stresses like crop pests and diseases as well as abiotic stresses such as droughts in traditional farming systems were among the major problems faced by the farmers leading to gradual replacement of traditional farmers' varieties. Genetic erosion is defined as "the loss of genetic diversity, in a particular location and over a particular period of time, including the loss of individual genes and the loss of particular combinations of genes such as those manifested in landraces or varieties" (FAO/IPGRI, 2002). It could be considered as a consequence of the loss of diversity in the farmer's field and will have a major effect on the future crop productions and productivity for indigenous crop species of Ethiopia. The problem has been increasing and is expected to be more aggravated for durum wheat than other cereal crops.

Several research reports from survey studies and farmers' discussion indicated loss of diversity on tetraploid wheat has increased faster than expected in different environments of Ethiopia. The reduction in number of farmers, traditional farmer varieties or landraces and area coverage confirmed the danger and extent of genetic erosion on tetraploid wheat, as reported in multiple studies. Teklu and Hammer (2006) reported genetic erosion of 88%, 100% and 78% for the durum wheat species *Triticum durum*, *T. turgidum* and *T. dicoccon*, respectively. In Harar Zuria, the same authors detected genetic erosion of 88.9 % for T. durum and 100% for both *T. turgidum* and *T. dicoccon*. In the western Shoa zone of Ethiopia, genetic erosion reached 75% and 62% for tetraploid wheat species in Ambo and Dandi districts, respectively (Geleta and Gausgruber, 2013). In a similar study farmers identified 26 tetraploid wheat land races (21 from Akaki and 17 from Ejere), which were once widely grown in the area and of which only six were currently available; the average loss of diversity was thus estimated to be 77% (Tsegaye and Berg, 2007). Besides primary sources collected from a survey using semi-structured questionnaires and farmers' group discussions, this study also used direct field assessment to identify recently cultivated landraces and compare them to previously available landraces in the similar districts, calculating levels of genetic integrity and erosion based on the procedures of Hammer *et al* (1996). The reduction in numbers of farmers growing landraces and area of cultivation were identified as useful indicators for the existence of genetic erosion (Brown and Hodgkin, 2015).

The objectives of this present study were to calculate and estimate on farm genetic erosion and identify associated causes in three districts of central Ethiopia using different approaches. Results obtained from direct field assessments and observations as well as information collected from farmers' interviews and discussions were used to investigate the current status of durum landraces and to determine trends based on the number of farmers using landraces and the area of cultivation of the landraces.

Materials and Methods

Study areas

The study was conducted in three districts of the central highlands of Ethiopia based on direct observation, a semi-structured survey questionnaire and group discussions. Direct observation was conducted across three different routes which covered Gimbichu, Ada, and Lume districts during the 2017 cropping season (Figure 1). A survey questionnaire and group discussions were conducted in Ada, Lume and Gimbichu districts of the central highlands of Ethiopia in 2018. The three districts were purposely selected to represent the durum wheat agro-ecology environment of the East Shoa Zone: 1) Ada represents a midland wheat growing agro-ecology area,where modern crop varieties are assumed to be dominantly cultivated; 2) Lume represents a midland area where both landraces and modern wheat cultivars are believed to exist due to interventions by the Ethiopian Biodiversity Institute to recover the status of local *in situ* conservation; and 3) Gimbichu district represents wheat growing agro-ecology at high elevation and is an area where durum landraces are still extensively cultivated.

Research methodology

Direct observations

Direct wheat field assessment and identification of species and varieties of species was conducted in November 2017 along three routes passing through major wheat producing districts in the central highlands of Ethiopia (Figure 1). The survey was made on 56 wheat growing farms at approximately three to five-kilometer intervals when the crop was observed. The different wheat species were classified into modern bread or durum and tetraploid landraces based on their spike characteristics and uniformity. The number of landraces available in 2017 compared to the landraces recorded in 1992 was the basis for calculating genetic integrity and genetic erosion. Modern wheat (bread and durum) and landraces area coverage was calculated as percentage of each wheat species area to the total wheat area of the 56 farms visited during direct farm assessment.

Survey study

A survey on perception on use of landraces and genetic erosion was carried out to collect data from149 farmers in three villages of the Ada, Gimbichu and Lume districts

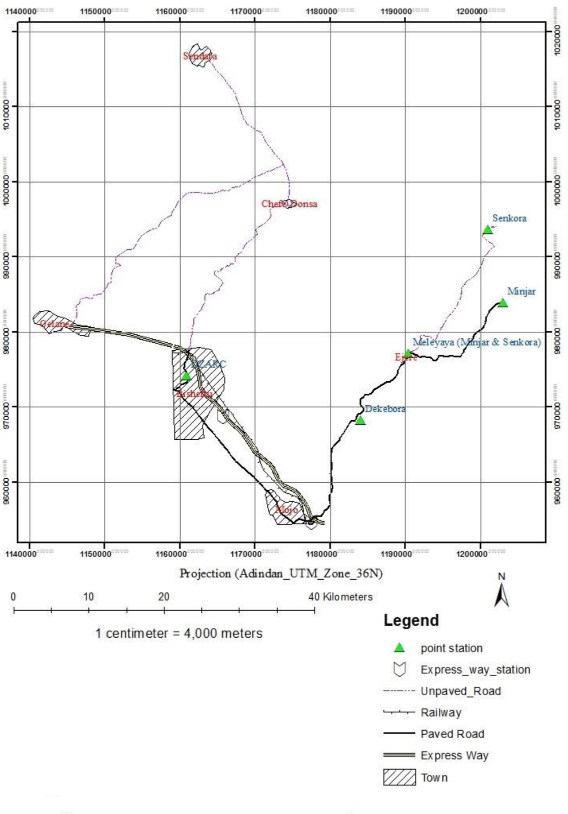

Figure 1. Travel routes for direct farm assessment.

using semi-structured questionnaires between10 and 25 December, 2018.

Group discussions

Farmers' group discussions were held in Ada, Gimbichu and Lume districts between 20 and 25 December 2018 to collect information about the past and current status of landraces and to identify causes why farmers stopped growing landraces in the area. Three group discussions in each district consisted of 12-15 systematically selected farmers from surrounding villages, also taking into consideration gender representation.

Data collection and summary

Genetic erosion was calculated according to the formula of Hammer *et al* (1996): GE = 100% - GI, where GE is genetic erosion and GI is genetic integrity, which is given as: $GI = N_2/N_1 \times 100$. The number of farmers cultivating landraces and their relative area coverage were determined. The number of landraces cultivated recently as compared to previous number was the basis for calculation of genetic erosion. In the present study, the number of landraces grown by the farmers 25 years ago (Negatu *et al*, 1992) was considered as N_1 and the number of landraces recorded in 2017 represented N_2.

Table 1. Genetic erosion on tetraploid wheat since 1992 in three districts of the central highlands of Ethiopia

Districts	landraces cultivated in 1992	landraces cultivated in 2017	Genetic Integrity (%)	Estimated genetic erosion (%)
Gimbichu	15	6	40	60
Lume	15	2	20	80
Ada	16	2	12.5	87.5

Results

Direct observation

Genetic erosion occurred on tetraploid wheat after 25 years based on direct farm assessment (Table 1). The variation was significant on loss of diversity on tetraploid wheat at 0.01%. The average genetic erosion across districts was 75.8%, which is lower compared to previous reports (Geleta and Gausgruber, 2013). The loss of diversity on tetraploid wheat was found to be the highest in Ada (87.5%) and lowest in Gimbichu (60%) based on direct field assessment (Table 1).

The proportion of landraces compared to modern wheat varieties was lower in lower altitude than high altitude growing environments (Figure 2). In 2017 the proportion of landraces in altitudes above 2400m were 70% while below 2400m this dropped to about 30% compared to modern wheat.

Number of farmers and area of cultivation

Modern bread and durum wheat as well as tetraploid landraces area coverage were estimated based on random field visits and identification of wheat species found in the field and calculated as percentage of each wheat species area to the total wheat area in a given district.

In 2017 only 8.3% of farmers in Lume, about 23.5% in Ada and 40.7% in Gimbichu were growing local varieties. When the three districts were considered, only

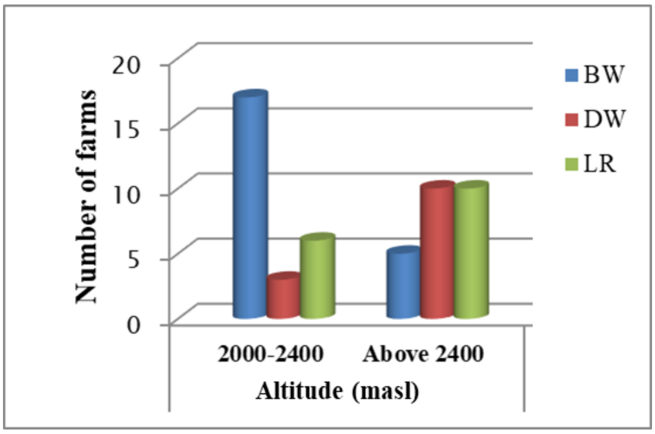

Figure 2. The number of tetraploid wheat (DW), local landraces (LR) and modern wheat varieties (BW) grown in different altitude zones based on direct field observations in 2017.

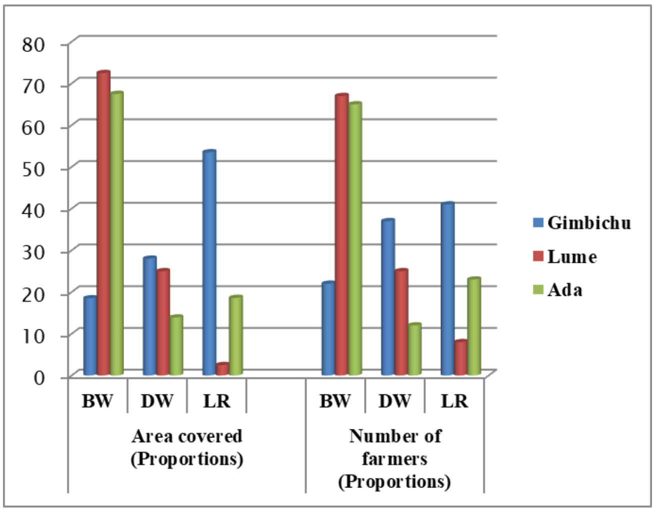

Figure 3. The proportion of landraces (LR), modern bread wheat (BW) and durum wheat (DW) varieties by area coverage and number of farmers in three Ethiopian districts in 2017 based on direct field observations on 56 farms in the districts.

24.2% of farmers were growing local durum wheat varieties. On average 24.5% of wheat growing area was occupied by landraces across the three districts compared to modern wheat varieties. The highest area coverage was in Gimbichu (52.3%) while the lowest was 2.5% in Lume (Figure 3).

Farmers' survey

In order to obtain a more pronounced picture of the estimated loss of genetic diversity in central Ethiopia, semi-structured interviews were conducted with 149 farmers from three communities in the three districts. Based on interviews with farmers, significant genetic erosion was observed in tetraploid wheat after 25 years (Table 2). The loss of diversity in tetraploid wheat reached up to 100% in Ada and was lowest in Gimbichu (67.7%), with an average of 87%, based on the survey.

In the 2018 growing season only 7.3% of farmers in the Lume district but 68.4% in Gimbichu were maintaining landraces of wheat. None of the farmers interviewed in Ada district were growing wheat landrace varieties. A similar trend was observed in cultivation area of landraces compared to modern varieties. The sample area coverage was 13.5% in Gimbichu and only 1.5% in Lume. No farms were cultivating landraces in Ada district (Figure 4).

Table 2. Genetic erosion of tetraploid wheat since 1992 in three districts of the central highlands of Ethiopia based on semi-structured interviews with 149 farmers.

Districts	Durum wheat varieties cultivated in 1992	Durum wheat varieties cultivated in 2017	Genetic Integrity (%)	Estimated genetic erosion (%)
Gimbichu	15	5	33.3	67.7
Lume	15	1	6.7	93.3
Ada	16	-	-	100.0

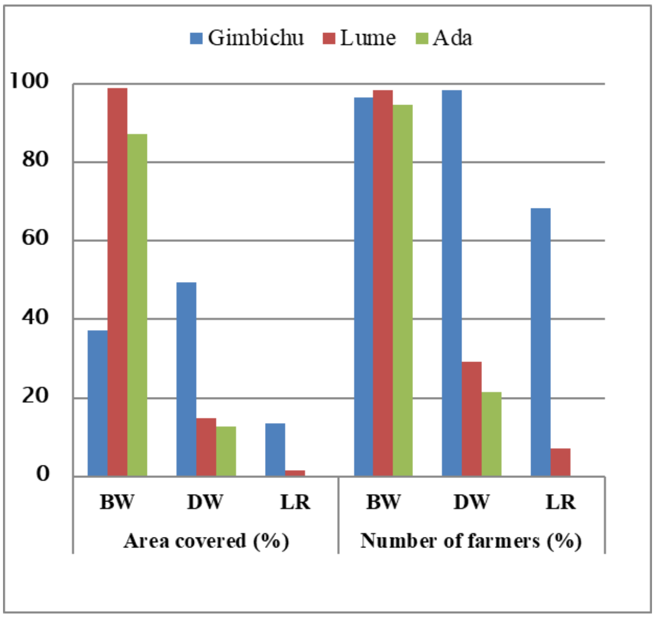

Figure 4. Percentage of landraces (LR) and modern bread wheat (BW) and durum wheat (DW) varieties by area coverage and number of farmers in three districts based on interviews with 149 farmers in 2018.

Group discussions

The reasons given by farmers on why they are currently not growing local varieties are presented in Table 3. The most common reason accounting for high losses in all three districts were identified as diseases and pests, mainly stem rust, followed by terminal drought associated with a short growing season. The data also indicated that the availability and supply of better yielding improved bread and durum varieties gradually replaced local varieties inducing farmers of these districts to stop or reduce growing local durum wheat varieties (Table 3). The expansion of high value crops like tef and chickpea was also mentioned as cause for losses of local varieties in Ada and Lume districts, whereas in Gimbichu water logging and the difficulty of using landraces for making local injera and bread due to its hard seed were raised as reasons for replacing landraces with modern wheat varieties. Similar findings and reasons were reported by Tsegaye and Berg (2007) in studies conducted in Lume and Akaki districts of the central highlands of Ethiopia.

On the contrary, the existence of a short growing season resulted in change in crop variety from farmers' to modern varieties that could be suited to early planting. Use of high amounts of fertilizer associated with growing modern varieties have resulted in shifting from landraces to modern varieties particularly in Ada and Lume districts where high genetic erosion was observed.

Table 3. Reasons for not growing local durum wheat landraces in 2018 in Ada, Lume, and Gimbichu districts, provided by farmers during the Group discussions.

Causes of genetic erosion	**Ada (N=37)**	**Lume (N=55)**	**Gimbichu (N=57)**	**All (N=149)**
Diseases and pests affecting landraces	15	48	36	99
Shorter growing season associated with climate change	13	27	21	61
Improved bread wheat	6	23	13	42
Improved durum wheat	4	15	20	39
Water logging	-	-	18	18
Unavailability of seed for the landraces	7	2	2	11
Utilization (durum landraces not suited for production of injera and bread)	-	-	6	6
Shortage of land and urbanization	5	-	-	5
Expansion of high value crops (tef and chickpea)	4	-	-	4

Discussion

The results indicated that on average 75.8% and 87% genetic erosion was observed on tetraploid wheat after 25 years based on direct farm assessment and survey study, respectively. The levels of loss observed from both approaches appear to be similar to that reported in Western Ethiopia (Geleta and Gausgruber, 2013). The loss observed was higher in Ada and Lume, situated at lower altitude, than in the high altitude zone above 2400 masl of Gimbichu district, where significant areas of land are still used to grow landraces. This difference can be attributed to the fact that both Ada and Lume districts have similar agro-ecology, access to big market centers and are also near to the Debre-Zeit Agricultural Research Center where a lot of improved wheat cultivars are developed, demonstrated and distributed. Modern wheat and tef crops are more expanded (Assefa *et al*, 2015) and could also be major causes for loss of diversity in the Ada and Lume districts. The presence of higher diversity in Gimbichu district might be associated to the merits of landrace adaptation and yield stability (Berg, 2009). Similarly, Tsegaye and Berg (2007) reported 77% genetic erosion and relative diversity for tetraploid wheat in Ejere, a high elevation district of central Ethiopia.

Our study demonstrated a correlation between the extent of genetic erosion and altitude. This indicates the relative importance of focusing further landrace collection and conservation efforts on altitudes above 2400 masl to capture more diversity. The study further confirmed the existence of better occupation in terms of area coverage and maintenance of landraces by large numbers of farmers in Gimbichu as compared to Ada and Lume. This could be due to the expansion of modern wheat varieties at the expense of the landraces in the latter districts as illustrated in Figure 3 and Figure 4 and confirmed by farmers' group discussions. Negatu *et al* (1992) reported that 64% of sample farmers grew local durum wheat varieties in the same districts of central Ethiopia. The low percentage of farmers currently growing local varieties in the three districts are likely the result of commendable expansion of well performing modern varieties.

The results found in the current survey and previous research reports were comparable to those obtained in direct farm assessment. The different approaches followed may account for the large variations observed on the extent of genetic erosion although the trends were similar between the altitudes. The findings of the study have a significant impact for *in situ* conservation of landraces for future use in breeding to combat the challenges of climate change. Farmers' opinions gathered in group discussions indicated that drought contributed to high loss of landraces in Ada and Lume and the result contradicts the existing theory that landraces are well adapted and coevolved in the environment they originated.

The results contribute to the setting of targeted strategies in high altitude zones for *in situ* conservation and exploitation of landraces in future breeding programs. Future studies should take into account direct observations as alternative approaches to assess and estimate genetic erosion of tetraploid wheat and other indigenous crop species.

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Author contributions

A. Zemede proposed, designed, and conducted the trial, analyzed data, drafted and finalized the manuscript. F.

Mekbib, K. Assefa and Z. Bishaw made valuable contributions to and commented on the final manuscript.

Conflict of interest statement

The authors declare that they have no competing interest.

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Morphometric and morphological characterization of chicken resources adapted to pastoral and agropastoral areas of southern Ethiopia

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Abstract: Thirteen qualitative and six quantitative variables taken from 303 adult chickens (95 cocks and 208 hens) from three locations/districts were used to phenotypically characterize the indigenous chicken populations in pastoral areas of South Omo Zone, Ethiopia. The studied traits were influenced by the effect of location and sex, where chicken populations from Hamer district and females of all districts were the smallest and lightest. Qualitative characteristics of the studied chicken populations such as normal feather morphology and distribution, plain plumage pattern, flat head shape, triangular body shape, and dominant red eye, earlobe and plumage colour suggest that they constitute previously undescribed populations. Chest circumference, wingspan and body length were the three most important morphometric traits used in discriminating the studied chicken populations. On average, 61% of the sampled populations were classified correctly into their respective locations. The multivariate analysis results discriminate the chicken populations into two groups: the Hamer group and the Omo group (chickens from Bena Tsemay and Male districts). However, such grouping should be confirmed and advanced to ecotype level using further genetic characterization studies as the observed phenotypic differences might be due to genetic or environmental variations. Such confirmation is important to design breeding programmes (for sustainable utilization) specific to each ecotype.

Keywords: Characterization, Chicken, Discrimination, Ethiopia, Indigenous, Multivariate

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Introduction

Ethiopia, which is believed to be the main gate for most of the indigenous animal genetic resources from Asia to Africa, is one of the countries that possess a large number of livestock populations across the globe (EBI, 2016). Chicken are the most widely distributed livestock species in Ethiopia (EBI, 2016) and worldwide (FAO, 2012). The estimated chicken population size of the country in 2018/2019 was 59.42 million (6 million cocks) among which 85.68% were indigenous (Central Statistical Agency, 2019).

Poultry production in Ethiopia is one of the key livestock subsectors which plays an important role in terms of creating employment, subsidizing women, and improving the nutritional content of food. Due to the relatively low investment costs and the small quantity of land required for starting and running poultry production, it has become a suitable business for low-income farmers (FAO, 2019). However, this subsector is not contributing with its full capacity due to poor productivity of and less attention given to indigenous chickens. Therefore, many exotic chicken breeds were disseminated in the country with the objective of increasing production and productivity, becoming the major threat to diversity due to the dilution of indigenous genetic resources and yet providing minimum effect on production and productivity.

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Genetic improvement and conservation as well as sustainable utilization of the resources can also be achieved through the application of within-breed selection-based breeding programmes (McDowell, 1972). Identification, characterization and documentation of the rich Ethiopian chicken genetic resources are a prerequisite for genetic improvement, breed conservation and sustainable utilization through designing suitable breeding programmes (FAO, 2012). Outputs of such studies will provide insight into variation within and between populations, which is one of the key contributions to conservation and genetic improvement programmes; it is more likely to maintain diversity and bring genetic improvement in a population with high variability. According to EBI (2016), Ethiopia possesses seven indigenous chicken ecotypes: the Farta, Horro, Jarso, Konso, Mandura, Tepi and Tillili.

The small number of indigenous chicken ecotypes reported in the country can be attributed to the lack of comprehensive identification and characterization work on the diversity and potential of Ethiopian chicken populations. In addition, limitations in methodology and a lack of concrete conclusions in terms of population differentiation were observed in most of the earlier characterization studies. For example, the region-wide chicken characterization study by Melesse and Negesse (2011) did not measure the most important linear measurements (wingspan, body length, chest and shank circumference) and failed to provide concrete conclusions.

Measuring, recording and reporting values without strong comparisons, discriminations and conclusions cannot be taken as an input in diversity studies of any given animal breed or ecotype. Therefore, there is an urgent need for continued characterization of indigenous chicken genetic resources to understand their potential and reveal the relationships within and among populations. A short pilot survey performed by a team of Ethiopian Biodiversity Institute (EBI) researchers and South Omo Zone and district livestock experts hinted at the presence of unique chicken populations, in South Omo Zone, Ethiopia, that was not described before. Thus, the present study was aimed at characterizing the chicken populations found in the area based on the FAO (2012) guidelines for characterization of animal genetic resources.

Materials and methods

Study areas

This study was conducted in South Omo Zone, which is found in the Southern Nations Nationalities and Peoples Regional State (SNNPR) and situated in the southern part of Ethiopia (Figure 1). The capital of South Omo Zone, Jinka, is 750 km south of the capital city of the country (Addis Ababa). The zone has a total area of 2,241,731.598 ha. The majority of the land is fertile and cultivated, with trees and bushes covering the remaining area. The zone falls in the arid and semi-arid category of the agroecological zone. Chickens are the most important animals for South Omo Zone pastoralists and agropastoralists next to ruminant animals (Tesfahun *et al*, 2017).

This study was conducted in three randomly selected pastoral and agropastoral districts (Bena Tsemay, Hamer and Male) of the eight districts found in the zone. Moreover, nine sampling sites (kebeles), three from each sampled district were selected based on the chicken population size data (Table 1). Two to three chicken were randomly selected for measurement from each randomly selected household within each kebele.

Study ecotypes

In literature, chicken populations of the current study area were generally classified as Konso chicken ecotypes (Dana *et al*, 2010). However, during the classification, samples were not taken from areas near the current study areas. Moreover, the results of our short pilot survey in South Omo Zone hinted at the presence of unique local chicken populations, which are different from Konso and were not described before. Furthermore, the studied chicken genetic resources are indigenous/local, producing, reproducing and surviving under the local environment since many years.

Data collection

The FAO guidelines for animal genetic resource characterization (FAO, 2012) were used to set the overall data collection procedures including the male to female ratio within the sampled chickens. The sampled chickens were randomly selected from flocks of representative households. Eleven qualitative traits (feather morphology and distribution, head shape, comb type and size, body shape, and colours of plumage body, earlobe, skin, shank, and eye), and six quantitative measurements (wingspan, body length, chest circumference, shank length, shank circumference, and live body weight) (Table 2) were recorded from 303 adult chicken (95 cocks and 208 hens) under the effect of district and sex.

During the measurements, animals were carefully handled by trained laborers and made to stand properly with parallel legs. The measurements were carried out by two researchers – one measuring and one recording data. At the same time, two other researchers handled the qualitative data recording. To minimize subjective error, all the measurements were taken by the same researcher throughout the study. Quantitative measurements were taken early in the morning before the animals were fed and watered using textile tape measures. Body weight was taken using sensitive digital weighing balances to the nearest of 0.05 g.

Data analysis

Data entry and management were performed using Microsoft Excel© worksheets. Analysis of the quantitative measurements was carried out separately for both sexes and sex aggregated by fitting district as class variable. The UNIVARIATE procedure of Statistical Analy-

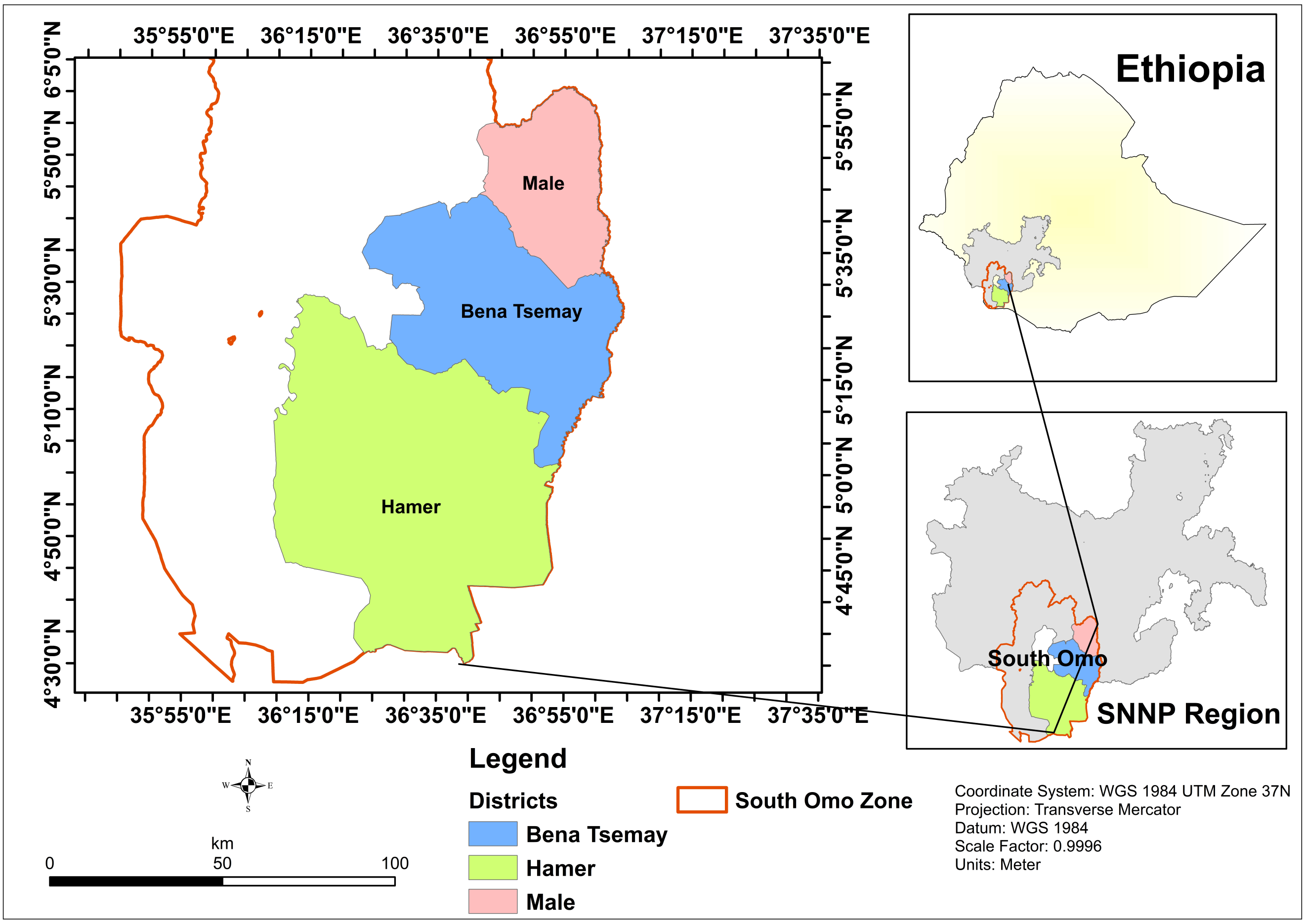

Figure 1. Map of the studied areas. The three study districts Bena Tsemay, Hamer and Male are located in South Omo, a zone within the Southern Nations Nationalities and Peoples Regional State (SNNP) in the southern part of Ethiopia.

sis Software (SAS) 9.0 (SAS Institute, 2002) was used to detect outliers and test the normality of the quantitative measurements data. Data on quantitative measurements and qualitative characteristics were analyzed using the General Linear Model (GLM) and the frequency (FREQ) procedures of SAS 9.0 software respectively. Least Square Means (LSM) of the linear measurements were separated using the adjusted Tukey-Kramer test (SAS Institute, 2002). Quantitative and qualitative data were analyzed using the following model: $Y_i = \mu + A_i + e_i$ where Y_i is an observation, μ is the overall mean, A_i is the fixed effect of district and e_i is the random error attributed to the nth observation.

Forward selection procedure of the stepwise discriminant function analysis (STEPDISC) was used to find out the quantitative variables that better discriminate populations from different districts. The canonical discriminant function analysis (CANDISC) was also used to find out linear combination of quantitative variables that provide maximal separations between the districts. Pairwise squared Mahalanobis distances between locations were computed as: $D^2\,(i|j) = (x_i - x_j)^{'}\, cov^{-1}\; (x_i - x_j)$. Where $D^2\,(i|j)$ is the distances between locations i and j, cov^{-1} is the inverse of the covariance matrix of measured variables, x_i and x_j are the means of variables in the i^{th} and j^{th} populations. The scored canonical variables were used to plot pairs of canonical variables

Table 1. Land use, climatic factors and chicken population size of the three studied districts. Data from Hidosa *et al* (2020); Hidosa and Tesfaye (2018); Gezahegn and Bamud (2018); Derib (2017).

Variables	Bena Tsemay	Hamer	Male
Land use	Agropastoralism	Pastoralism	Agropastoralism
Altitude (m)	500 – 1800	450 – 1765	600 – 1500
Temperature (°C)	17.3 – 28.9	29 – 38	18 – 35
Annual rainfall (mm)	1,167	400	800 – 1200
Chicken population size	94,056	54,288	226,904

Table 2. Six quantitative measurements definition and description of measuring devices used to characterize chicken populations. Adapted from FAO (2012).

No.	Linear traits	Definition of quantitative morphological variables	Unit	Measuring device
1	Wingspan	Length between tips of right and left wings after both are stretched out in full	cm	Measuring tape
2	Body length	Length between the tip of the rostrum maxillare (beak) and that of the cauda (tail, without feathers); the bird's body should be completely drawn throughout its length	cm	Measuring tape
3	Chest circumference	Taken at the tip of the pectus (hind breast)	cm	Measuring tape
4	Shank length	Length of the shank from the hock joint to the spur of either leg	cm	Measuring tape
5	Shank circumference	Taken at the middle of the shank of either leg	cm	Measuring tape
6	Body weight	Live body weight	g	Digital balance

to get visual interpretation of district differences. Percentage assignment of observations to known geographical locations (districts) and probabilities of misclassifications were evaluated by discriminant function analysis (DISCRIM).

Results

Quantitative measurements

Level of significance (P values) outputs for the effect of district and sex on the quantitative measurements analyzed for the chicken populations as a whole and separately for each sex are presented in Table 3. Results of the overall analysis show a significant effect of sex on the studied traits with dominance of cocks on all measured traits. Similarly, all studied traits were affected significantly by district in the sex-aggregated analysis. However, effect of district on wingspan and shank circumference was variable due to individuals' sex, where the cocks' wingspan and the hens' shank circumference were not significantly different across districts.

Least square means with the respective standard errors (LSM±SE) for the effect of district on the quantitative measurements of the chicken populations as a whole and separately for each sex are presented in Table 4. Cocks from Hamer district have the lowest values except for wingspan, while their counterparts from Bena Tsemay and Male districts were not significantly different in the measured traits. Body length, chest circumference, shank length and body weight of the Hamer hens were also lower than their counterparts from the other districts.

Qualitative characteristics

The hypothesis whether the qualitative characteristics of the studied chicken populations differ across districts and sexes was tested using chi-squared analysis. The results presented in Table 5 showed a significant effect of district and sex on most of the qualitative characteristics. The colour-related traits except earlobe colour of the cocks were significantly affected by district.

The percentages of qualitative characteristics in each district are presented in Table 6 and Table 7. Accordingly, silky feather morphology was observed on Bena Tsemay cocks. The majority of Bena Tsemay cocks possess single comb while one-fourth of the Male and Hamer cocks have a double comb type. The rectangular body shape was observed on almost half of the Bena Tsemay cocks, while the triangular body shape was dominant on cocks from other districts. All Hamer hens possess triangular body shapes while one-fourth of the Bena Tsemay hens had rectangular body shapes. The majority of the studied chicken populations have been characterized by normal feather morphology and distribution, plain plumage pattern, flat head shape, single comb type, and triangular body shape. The comb size of the studied chicken populations was sex-dependent; the majority of hens had small combs while cocks had medium-sized combs. The spur was also absent in the majority of hens from all districts.

Red plumage, earlobe and eye colour combined with yellow skin and shank colour, were dominantly observed in cocks from all districts (Table 7). On the other hand, red earlobe and eye colour with yellow shank colour were observed in the majority of hens in all districts. The majority of chickens in the Bena Tsemay and Male districts had yellow shank colour, while chicken populations from Hamer district had a large proportion with grey shank colour. Similarly, the skin colour of most of the chicken population from this study were yellow and white, with grey skin colour observed only in Hamer hens (18.6%). The plumage body colour of Male and Hamer hens was dominated by grey colour while brown, red and black were observed in the majority of Bena Tsemay hens.

Multivariate analysis for discrimination of chicken populations

Stepwise discriminant analysis

Six quantitative measurements for both sexes were separately subjected to the STEPDISC procedure of SAS 9.0. Accordingly, all measurements in cocks and five measurements in hens were identified as the best discriminatory variables. These results were confirmed by Wilk's lambda test (Table 8) where all selected variables had highly significant ($P<0.0001$) contribution

Table 3. Level of significance for the overallanalysis and separately for each sex. WS = Wingspan, BL = Body length, CC = Chest circumference, SL = Shank length, SC = Shank circumference, BW = Body weight, *p<0.05, **p<0.01, ***p<0.0001, NS = Not Significant, CV = Coefficient of variation.

Traits	Overall chickens			Cocks		Hens	
	District	Sex	CV	District	CV	District	CV
WS	**	***	8.35	NS	7.63	*	8.76
BL	***	***	6.88	***	6.49	***	7.08
CC	***	***	9.25	***	9.85	***	8.79
SL	***	***	10.16	**	8.45	**	11.05
SC	**	***	10.56	**	12.19	NS	9.27
BW	***	***	21.60	**	22.93	***	20.34

Table 4. Pairwise mean comparison (least square means and standard errors (LSM±SE)) for the effect of district within each sex. Means within a column bearing different superscripts are significantly different; a is given to the highest value. N = number of observations, WS = Wingspan, BL = Body length, CC = Chest circumference, SL = Shank length, SC = Shank circumference, BW = Body weight.

Traits	District		
	Bena Tsemay	Male	Hamer
Cocks			
N	37	30	28
WS (cm)	41.14±0.52	41.13±0.58	42.86±0.60
BL (cm)	42.30±0.44^{a}	42.00±0.49^{a}	39.00±0.51^{b}
CC (cm)	30.05±0.48^{a}	31.37±0.53^{a}	27.36±0.55^{b}
SL (cm)	9.92±0.14^{a}	10.37±0.15^{a}	9.39±0.16^{b}
SC (cm)	4.92±0.10^{a}	5.00±0.11^{a}	4.50±0.11^{b}
BW (g)	1695.89±62.92^{a}	1859.63±69.88^{a}	1428.86±72.33^{b}
Hens			
N	95	70	43
WS (cm)	36.06±0.32^{ab}	35.50±0.38^{b}	37.23±0.48^{a}
BL (cm)	38.09±0.27^{a}	36.94±0.31^{b}	35.02±0.40^{c}
CC (cm)	27.91±0.25^{a}	27.67±0.29^{a}	25.79±0.37^{b}
SL (cm)	8.28±0.09^{a}	8.26±0.10^{a}	7.67±0.14^{b}
SC (cm)	4.17±0.04	4.20±0.05	4.04±0.06
BW (g)	1373.87±27.78^{a}	1400.16±32.36^{a}	1124.23±41.29^{b}
Both sexes			
N	132	100	71
WS (cm)	38.67±0.29^{b}	38.27±0.33^{b}	40.02±0.38^{a}
BL (cm)	40.24±0.24^{a}	39.34±0.27^{b}	37.06±0.32^{c}
CC (cm)	29.06±0.24^{a}	29.28±0.27^{a}	26.67±0.31^{b}
SL (cm)	9.14±0.08^{a}	9.25±0.09^{a}	8.54±0.11^{b}
SC (cm)	4.53±0.04^{a}	4.58±0.05^{a}	4.30±0.06^{b}
BW (g)	1543.70±28.31^{a}	1610.42±31.98^{a}	1282.62±37.06^{b}

in discriminating the chicken populations into separate groups. The stepwise discriminant function analysis also revealed that chest circumference, wingspan and body length were the three most important morphometric traits used in discriminating the chicken populations from different districts. However, body length, wingspan and body weight were the three most important variables used to discriminate the hens from different districts. Shank circumference was found to be less useful in discriminating the overall chicken populations due to its lowest discriminatory power (Table 8).

Discriminant analysis

The multivariate statistics and F approximations used in discriminating the studied chicken populations (cocks, hens and both sexes) are presented in Table 9. Accordingly, all the statistics used in discriminating the populations were significant. Higher F and Den DF values were calculated as the number of observations increased.

Results of a discriminant function analysis (Table 10) show the overall classification of individuals into a known location/district. Accordingly, the correct

Table 5. Chi-square values and probabilities for the effect of classes on qualitative characteristics for the overall analysis and separately for both sexes. X^2 = chi-square value; P = probabilities; *p<0.05, **p<0.01, ***p<0.0001, NS = Not Significant.

Qualitative traits	Overall				Cocks		Hens	
	District		Sex		District		District	
	X^2	P	X^2	P	X^2	P	X^2	P
Feather morphology	7.93	*	13.40	**	10.04	**	-	-
Feather distribution	7.91	NS	3.00	NS	3.20	NS	5.05	NS
Plumage pattern	5.25	NS	1.85	NS	-	-	4.85	NS
Head shape	8.65	NS	3.19	NS	2.66	NS	6.79	NS
Comb type	25.35	**	22.53	**	17.34	**	12.99	NS
Comb size	3.73	NS	135.2	***	5.43	NS	7.48	NS
Body shape	27.72	***	8.41	*	11.06	*	24.14	***
Spur presence	3.16	NS	118.6	***	2.51	NS	7.32	*
Plumage colour	36.13	***	50.70	***	22.18	*	26.09	**
Earlobe colour	17.38	**	20.24	**	6.55	NS	16.57	*
Skin colour	49.06	***	17.87	***	6.71	*	49.90	***
Shank colour	52.07	***	17.73	**	27.69	**	40.17	***
Eye colour	80.30	***	5.50	NS	30.03	***	57.02	***

Table 6. Percentages for the qualitative characteristics of the chicken populations from different districts.

Qualitative traits	Cocks			Hens		
	Bena Tsemay	Male	Hamer	Bena Tsemay	Male	Hamer
Feather morphology						
Normal	83.8	100	100	100	100	100
Silky	16.2	0	0	0	0	0
Feather distribution						
Normal	94.6	100	100	91.6	94.3	97.7
Naked neck	5.4	0	0	6.3	1.4	2.3
Crest	0	0	0	2.1	4.3	0
Plumage pattern						
Plain	100	100	100	95.8	100	100
Barred	0	0	0	3.2	0	0
Barring	0	0	0	1.0	0	0
Head shape						
Flat	100	96.7	92.9	92.6	98.6	95.4
Crust	0	0	0	5.3	1.4	0
Snake	0	3.3	7.1	2.1	0	4.6
Comb type						
Single	86.5	63.3	53.6	75.8	58.6	62.8
Pea	2.7	0	14.3	8.4	18.6	16.3
Rose	10.8	16.7	10.7	12.6	20.0	18.6
V-shape	0	0	0	3.2	0	0
Double	0	20.0	21.4	0	2.8	2.3
Comb size						
Small	35.1	20.0	21.4	85.3	97.1	93.0
Medium	37.9	53.3	64.3	13.7	2.9	7.0
Large	27.0	26.7	14.3	1.0	0	0
Body shape						
Blocky	0	3.3	0	2.1	0	0
Rectangular	45.9	16.7	17.9	26.3	7.1	0
Triangular	54.1	80.0	82.1	71.6	92.9	100
Spur presence						
Absent	27.0	43.3	42.9	89.5	98.6	97.7
Present	73.0	56.7	57.1	10.5	1.4	2.3

Table 7. Percentages of some colour-related qualitative traits of the chicken populations from different districts.

Qualitative traits	Cocks			Hens		
	Bena Tsemay	Male	Hamer	Bena Tsemay	Male	Hamer
Plumage colour						
Black	5.4	0	0	20.0	11.4	9.3
Brown	5.4	0	0	25.3	17.2	9.3
Grey	10.8	30.0	17.9	15.8	30.0	44.2
Red + White	8.1	10.0	25.0	1.0	7.1	11.6
Red	46.0	56.7	53.6	25.3	18.6	16.3
White	24.3	3.3	3.6	12.6	15.7	9.3
Earlobe colour						
White	5.6	6.7	3.6	15.0	18.6	32.6
Red	88.8	66.6	71.4	77.5	72.8	51.1
Red + White	5.6	26.7	25.0	3.8	4.3	16.3
Black	0	0	0	3.7	4.3	0
Skin colour						
Grey	0	0	0	0	0	18.6
White	43.2	16.7	21.4	63.2	31.4	48.8
Yellow	56.8	83.3	78.6	36.8	68.6	32.6
Shank colour						
Yellow	91.9	96.7	50.0	56.8	70.0	37.2
Black	2.7	0	10.7	20.0	12.9	16.3
White	5.4	3.3	17.9	20.0	4.3	9.3
Grey	0	0	21.4	3.2	12.8	37.2
Eye colour						
Red	62.2	100	92.9	73.7	95.7	72.1
Blue	0	0	7.1	0	0	7.0
Brown	0	0	0	1.0	2.9	18.6
White	5.4	0	0	3.2	0	2.3
Yellow	32.4	0	0	22.1	1.4	0

classification of cocks into their location/district ranged from 51% in Bena Tsemay to 75% in Hamer. The overall average error rate was 39%, and 61% of the individuals were classified correctly. An average of 64% and 58% of the sampled cocks and hens were classified correctly into their corresponding districts, respectively. A higher error rate of 55% was observed in Bena Tsemay hens, while a lower error rate (23%) was obtained from the classification of Hamer district hens.

Canonical discriminant analysis

Different multivariate statistics (including canonical correlation and eigenvalues), the coefficient values for each trait used, and class mean outputs using the first two canonical structures are shown in Table 11. The first canonical structure (Can 1) explains the majority (85.4%) of the variability among the three districts (84.5% for cocks and 84.3% for hens). Can 1 also produces the greatest multiple correlation (60.2%) with the classes that was achieved by using the linear combination of the quantitative traits; the values were 72.7% for cocks and 55.5% for hens. The results revealed that Can 1 separates the chicken populations (class means) from different districts better than Can 2.

The pairwise squared Mahalanobis distances between locations/districts for analysis groups presented in Table 12 were highly significant (P<0.0001). The shortest distance (0.6) was calculated between the chicken populations of Bena Tsemay and Male districts; 1.36 for cocks and 0.46 for hens. On the other hand, the chicken populations from Hamer district were more distantly related to the others (2.87 and 3.71 from Bena Tsemay and Male districts, respectively).

Discussion

Quantitative measurements

The quantitative measurements taken have produced reliable information on characterization, evaluation and differentiation of the studied chicken populations. In line with most reports, these measurements were significantly affected by the location sampled. The longest wings and smallest body size of the Hamer chickens make them significantly different from the chicken populations of the other two locations. These long wings stretched from the small body size can be recorded and reported as the unique characteristics

Table 8. Summary of the stepwise discriminant function analysis; ascending order of traits used in discriminating the chicken populations from different districts.

Group	Step	Variable entered	Partial R-Square	F value	P>F	Wilks' Lambda	P<Lambda
Cocks							
	1	Chest circumference	0.2353	14.15	<0.0001	0.7647	<0.0001
	2	Wingspan	0.1907	10.72	<0.0001	0.6189	<0.0001
	3	Body length	0.1886	10.46	<0.0001	0.5022	<0.0001
	4	Shank length	0.1267	6.46	0.0024	0.4386	<0.0001
	5	Body weight	0.0568	2.65	0.0764	0.4137	<0.0001
	6	Shank circumference	0.0542	2.49	0.0884	0.3912	<0.0001
Hens							
	1	Body length	0.1661	20.42	<0.0001	0.8339	<0.0001
	2	Wingspan	0.0877	9.80	<0.0001	0.7608	<0.0001
	3	Body weight	0.1162	13.34	<0.0001	0.6724	<0.0001
	4	Shank length	0.0366	3.84	0.0231	0.6478	<0.0001
	5	Chest circumference	0.0207	2.13	0.1220	0.6344	<0.0001
	-	Shank circumference	0.0005	0.05	0.9498	-	-
Both sexes							
	1	Chest circumference	0.1006	16.78	<0.0001	0.8994	<0.0001
	2	Wingspan	0.1890	34.83	<0.0001	0.7294	<0.0001
	3	Body length	0.1068	17.82	<0.0001	0.6515	<0.0001
	4	Body weight	0.0637	10.10	<0.0001	0.6100	<0.0001
	5	Shank length	0.0523	8.17	0.0004	0.5781	<0.0001
	-	Shank circumference	0.0005	0.08	0.9259	-	-

Table 9. Multivariate statistics and F approximations used in discrimination of the chicken populations. DF = degrees of freedom; P = Probability.

Group	Statistic	Value	F value	DF	Den DF	P>F
Cocks						
	Wilks' Lambda	0.3912	8.68	12	174	<0.0001
	Pillai's Trace	0.6986	7.87	12	176	<0.0001
	Hotelling-Lawley Trace	1.3265	9.54	12	132.28	<0.0001
	Roy's Greatest Root	1.1217	16.45	6	88	<0.0001
Hens						
	Wilks' Lambda	0.6340	8.53	12	400	<0.0001
	Pillai's Trace	0.3916	8.16	12	402	<0.0001
	Hotelling-Lawley Trace	0.5367	8.91	12	308.04	<0.0001
	Roy's Greatest Root	0.4459	14.94	6	201	<0.0001
Both sexes						
	Wilks' Lambda	0.5778	15.51	12	590	<0.0001
	Pillai's Trace	0.4560	14.57	12	592	<0.0001
	Hotelling-Lawley Trace	0.6722	16.48	12	455.81	<0.0001
	Roy's Greatest Root	0.5696	28.10	6	296	<0.0001

of Hamer chickens, which might be related to their mothering ability.

A previous study by Dana *et al* (2010) which describes Konso as a chicken ecotype took only two quantitative measurements (the body weight and shank length). In terms of body weight both cocks and hens of the current study were heavier than the Konso chicken ecotype where the body weights of the Konso cocks and hens were 1,411 g and 1,011 g respectively (Dana *et al*, 2010). Such phenotypic variations in body weight hint at the presence of genetic diversity that needs to be conserved and can also be used as a base in attaining genetic improvement through selection. Therefore, in terms of body weight, the current chicken populations were different from the Konso chicken ecotype.

On the other hand, their shank length measurements were comparable. According to Melesse and Negesse (2011), the shank length is considered a good indicator of adaptation to lowland areas and skeletal development, which is related to the amount of meat a chicken

Table 10. Number and (percent) of observations classified into districts.

Group	From district	Bena Tsemay	Hamer	Male	Total
Cocks					
	Bena Tsemay	19 (51%)	7 (19%)	11 (30%)	37 (100%)
	Hamer	3 (11%)	21 (75%)	4 (14%)	28 (100%)
	Male	8 (27%)	2 (7%)	20 (66%)	30 (100%)
	Total	30 (32%)	30 (32%)	35 (36%)	95 (100%)
	Error rate	49%	25%	34%	36%
Hens					
	Bena Tsemay	43 (45%)	18 (19%)	34 (36%)	95 (100%)
	Hamer	5 (11%)	33 (77%)	5 (11%)	43 (100%)
	Male	24 (34%)	9 (13%)	37 (53%)	70 (100%)
	Total	72 (35%)	60 (29%)	76 (36%)	208 (100%)
	Error rate	55%	23%	47%	42%
Both sexes					
	Bena Tsemay	65 (49%)	22 (17%)	45 (34%)	132 (100%)
	Hamer	9 (13%)	52 (73%)	10 (14%)	71 (100%)
	Male	31 (31%)	8 (8%)	61 (61%)	100 (100%)
	Total	105 (35%)	82 (27%)	116 (38%)	303 (100%)
	Error rate	51%	27%	39%	39%

Table 11. Multivariate statistics, canonical coefficients of the quantitative variables, and class means outputs of the two canonical structures separately for each sex. Can = Canonical structure.

	Cocks		Hens		Both sexes	
	Can 1	Can 2	Can 1	Can 2	Can 1	Can 2
Multivariate statistics						
Canonical correlation	0.7271	0.4122	0.5553	0.2885	0.6024	0.3051
Eigenvalue	1.1217	0.2047	0.4459	0.0908	0.5696	0.1026
Proportion	0.8457	0.1543	0.8309	0.1691	0.8473	0.1527
Cumulative	0.8457	1.0000	0.8309	1.0000	0.8473	1.0000
F value	8.68	3.60	8.53	3.65	15.51	6.08
P>F	<0.0001	0.0052	<0.0001	0.0035	<0.0001	<0.0001
Traits						
Wingspan	-0.3191	0.0338	-0.2780	0.1110	-0.3280	0.0350
Body weight	0.0004	-0.0029	0.0019	-0.0031	0.0015	-0.0028
Body length	0.1247	0.5403	0.0915	0.4719	0.0560	0.5070
Chest circumference	0.1727	-0.0725	0.1483	0.0356	0.1828	0.0089
Shank length	0.5074	-0.8638	0.3943	-0.5278	0.3388	-0.7575
Shank circumference	0.4542	0.8747	-0.1134	0.0512	-0.0147	0.1737
Class (district) mean						
Bena Tsemay	0.4234	0.5273	0.3164	0.2933	0.2980	0.3400
Male	0.9488	-0.5150	0.3679	-0.3858	0.5594	-0.3871
Hamer	-1.5761	-0.1450	-1.298	-0.0200	-1.3419	-0.0869

can carry. This shows their high adaptability to the lowland areas of the pastoral and agropastoral community.

Comparable, higher and lower values of wingspan, body length, chest circumference, shank length and shank circumference measurements were reported in indigenous chickens in different parts of the country. However, surprisingly low values were also reported. For example, Negassa *et al* (2014) reported 7.35–8.17 cm of wingspan and 22.6–24.2 cm of body length for chickens in southeastern Ethiopia. Similarly, Halima *et al* (2007) reported 12.67–15.83 cm of wingspan and 0.53–0.93 cm of shank circumference for chickens in northern Ethiopia.

Effect of sex

Cocks were bigger and heavier than hens, which follows Rensch's rule (Rensch, 1950) where the males of an individual species are generally larger than the females. Such differences between cocks and hens may be attributed to the differences in hormone secretion,

Table 12. Squared Mahalanobis distance between districts; output of the multivariate analysis calculated using the quantitative measurements. *** indicates significance of the distance calculations at $p<0.0001$.

Group	From district	Bena Tsemay	Male	Hamer
Cocks				
	Bena Tsemay	**0**		
	Male	1.36**	**0**	
	Hamer	4.45***	6.51***	**0**
Hens				
	Bena Tsemay	**0**		
	Male	0.46**	**0**	
	Hamer	2.70***	2.91***	**0**
Both sexes				
	Bena Tsemay	**0**		
	Male	0.60***	**0**	
	Hamer	2.87***	3.71***	**0**

which leads to enlargement of muscle mass and skeletal development (Baneh and Hafezian, 2009). These results were in line with the reports of Bekele *et al* (2015), Getu *et al* (2014), Negassa *et al* (2014), and Melesse and Negesse (2011), Dana *et al* (2010) and Halima *et al* (2007) on different indigenous chicken populations of Ethiopia. Similarly, sexual dimorphism was reported for most traits with males having higher values when compared to the females in other species of Ethiopia, including goats (Mustefa *et al*, 2019), cattle (Mustefa *et al* (2020b)), donkeys (Mustefa *et al* (2020a)) and sheep (Hailu *et al*, 2020).

Qualitative characteristics

Observable qualitative characteristics, in addition to the quantitative measurements, have allowed us to characterize, identify and differentiate the studied chicken populations. Dana *et al* (2010), Bekele *et al* (2015), Melesse and Negesse (2011) reported normal feather morphology and distribution in the majority of indigenous chicken populations in Ethiopia's southern region that are comparable with the results of the current study. Melesse (2000) described the naked-neck gene as one of the main genes responsible for heat tolerance of some Ethiopian indigenous chicken populations by improving and enhancing heat dissipation due to the reduction in feather coverage. However, the current study also revealed the adaptation of indigenous chickens to the local pastoral and agropastoral lowland areas with a lower frequency of naked-neck chickens. This lower frequency of naked-neck chicken in the current study area specifically, as well as in the country in general, may also be a factor for their poor productivity (Ajang *et al*, 1993). Similarly, Yunis and Cahaner (1999) reported the probability of attaining higher egg and/or meat production in chicken with reduced feathering due to the saved feather protein.

Qualitative deviations were also observed between Konso ecotype and the current chicken populations. Firstly, the comb types, which vary greatly depending on the breed, are also a great indicator of a chicken's health. Bright fleshy combs indicate physical strength and good health. Combs also help chickens regulate their body temperature – those with large combs are able to circulate blood faster through their combs, which helps to release body heat. This is why chickens adapted to warm environments have larger combs (like single combs and buttercup combs) while breeds from colder areas have smaller combs (like pea and rose combs) (Vaughn, 2019). The majority of chickens from the current study area were single-combed while Dana *et al* (2010) reported a higher frequency of pea-combed chickens in the Konso chicken ecotype. Dana *et al* (2010) also reported humid lowland to wet highland ecological zones as local areas of the Konso chicken ecotype. The comb size of the studied chicken populations was found to be sex-dependent where hens of a given population had smaller combs than the cocks. This was supported by Bell (2002) who reported the association of comb size with gonadal development and intensity of light.

The earlobe colour of a chicken can determine the colour of the egg that it will lay. For example, if the chicken has a red earlobe, it will lay a brown-shelled egg and if it has a white earlobe, it will lay a white-shelled egg (Bell, 2002). Red earlobe colour was observed in the majority of chickens from the current study, while Dana *et al* (2010) reported equal frequency of red and white earlobe colours in Konso chicken ecotype. The observation of a higher proportion of hens with white earlobe colour than the cocks in each district was due to the sex-linked nature of the trait (Luo *et al*, 2018). Among the populations of the current study, a higher proportion of white earlobes was observed in Hamer hens than the others, which might be due to their distinction from the others as earlobe colour is a breed-specific trait, though it could also be affected by the nutritional status of the chicken populations (Melesse and Negesse, 2011).

The triangular body shape was dominantly found in the current study while the results of Dana *et al* (2010) reported blocky body shape for the majority of the Konso chicken ecotype. On the other hand, similar qualitative characteristics, like flat head shape, were observed on both Konso chicken ecotypes (Dana *et al*, 2010) and the current chicken populations.

Chicken populations, breeds and breeding groups can be identified by their plumage colours due to their decorative qualities. Plumage colour is also a key trait during the interaction of chickens due to their well-developed visual perception of the world (Makarova *et al*, 2019). In agreement with most Ethiopian reports, several plumage colours were found in the current study area with a higher frequency of red-coloured cocks. On the other hand, the predominance of grey (faded white and black) colour observed in hens is in line with the reports of Halima *et al* (2007). The diverse plumage colours in the current study, which might be due to either genetic or environmental factors, showed the presence of diverse genetic resources, which can be an input in conservation and genetic improvement programmes for sustainable use.

Bekele *et al* (2015), Getu *et al* (2014), Halima *et al* (2007), Dana *et al* (2010) reported yellow as the most widespread shank and skin colour in different indigenous chicken populations of Ethiopia, which agrees with the current findings. According to Hammond and Harshaw (1941), a chicken's shank and skin colour are influenced by breed, quantity of xanthophyll pigment in the diet, and quantity of a pigmentation-suppressing factor in the diet. Bell (2002) stated that yellow shank colour is due to nutritional carotenoid colourants in the epidermis when the melanic pigment is absent. Similarly, variable shades of black colour are the result of melanic pigment in the dermis and epidermis; if the black colourant is in the dermis and yellow in the epidermis, greenish shanks will appear. However, if both these pigments are completely absent, the shanks will be white (Bell, 2002).

Commonly, red, yellow and black eye colours are due to the three pigments in the form of hemoglobin, carotenoids and melanin respectively. Red eye colour is influenced by the degree of iridic vessels injection and hemoglobin content of the blood (Nelson, 1947). According to Nelson (1947), when chickens suffer from general anemia, a smaller amount of red colouration will be noted due to loss of blood volume. Therefore, the dominant red eye colour observed in the current study is a confirmation that these chicken populations were free from such suffering. As per the same author, continual egg production can decrease the yellow factor in eye colour. Therefore, the yellow eye colour chicken from Bena Tsemay district (27%) might indicate restrictions in egg productivity.

Multivariate analysis

The use of more quantitative measurements during the discrimination analysis approaches the results towards reality. This is supported by the current results, where only one quantitative measurement in hens had low discriminatory power.

In line with reports by Mustefa *et al* (2020b) on Raya cattle (61%) and Hailu *et al* (2020) on Tigray sheep (66%), the discriminant function analysis allowed the classification of an average 61% of the studied individuals into their respective locations. The observed highest classifications of individuals into their respective districts in Hamer cocks and hens (75% and 77% respectively) showed their distinctness from the others due to the unique characteristics they possess. However, the lowest classifications (45% and 53%) were recorded in hens from Bena Tsemay and Male district indicating strong similarities between them.

The highly significant and longest pairwise Mahalanobis distances between districts indicate the accuracy of the calculations and the distinctness of the populations from each other in a measurable group difference for the considered quantitative measurements. Accordingly, the longest distances of Hamer chickens from the other two chicken populations in this study showed its distinctness.

In conclusion, the main contribution of this diversity study is the provision of information and data for breed differentiation, conservation and sustainable utilization of the chicken ecotypes in the districts, as well as the collation of information and data available on chicken ecotypes of Ethiopia. Accordingly, the chicken populations can be categorized phenotypically into two groups: the Hamer group and the Omo group (which includes the indigenous chicken populations from Bena Tsemay and Male districts). However, such differences in phenotypic performances might be either due to genetic or environmental variations. Therefore, we cannot conclude that the differences are solely due to genetic variations. Thus, genetic characterization is recommended to understand their potential and the within- and among-population genetic diversity and population structures.

Data availability

As baseline data for further research and development work, these data will be made available in the country's focal institute for indigenous animal genetic resources, the Ethiopian Biodiversity Institute (EBI) and the global Domestic Animal Diversity Information System (DAD-IS) databases.

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Author contributions

All authors contributed to the study conception and design. Material preparation and data collection were performed by Amine Mustefa, Hizkel Kenfo, and Teklewold Belayhun. Data analysis and writing the first draft of the manuscript was performed by Amine Mustefa and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Conflict of interest statement

The authors declare no conflict of interest.

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