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ORIGINAL PAPER

Comparative analysis of the gene pool structure of *Triticum aethiopicum* wheat accessions conserved ex situ and recollected in fields after 85 years

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Abstract

A molecular marker approach was used to analyse the genetic diversity of endemic *Triticum aethiopicum* wheat accessions that were collected from the same sites in Ethiopia by N.I. Vavilov in 1927 and by the Joint Ethiopian-Russian Biological Expedition in 2012, which allowed the assessment of changes in the gene pool structure of this species over 85 years. The level of genetic diversity in the accessions from Vavilov's collection was higher than that of the accessions collected in 2012. Analysis of molecular variance indicated that differentiation between the two groups of accessions was 17% ($PhiPT = 0.169$; $p < 0.010$). A Bayesian clustering approach and principal coordinates analysis showed that these two groups of accessions were notably different in their genetics. In this regard, this article discusses the problem of in situ and ex situ conservation of wheat landraces: their evolution, stability and genetic drift.

Keywords Biodiversity · *Triticum aethiopicum* · AFLP analysis

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Introduction

Agricultural biodiversity is an important component of total biodiversity and is of major importance for agriculture and food production. As such, there is increasingly more data about changes in the levels of genetic diversity in cultivated plants (Fu et al. 2003; Khlestkina et al. 2004, 2006; Metakovsky et al. 2019), as well as their relatives (Gao et al. 2000; Thormann et al. 2017). The loss of variation in crops, which has been described as genetic erosion, due to the modernisation of agriculture is of particular concern (van de Wouw et al. 2009). A solution to the problem of genetic erosion is the preservation of cultivated plant genetic resources (Dulloo et al. 2010; Halewood 2013). Two basic strategies for preserving genetic biodiversity exist. They are in situ and ex situ conservation (CBD 1992; Maxted et al. 2008). The first half of the twentieth century was characterised by many expeditions, such as N.I. Vavilov's expedition (Vavilov et al. 1931) to collect landraces of cultivated plants. These expeditions have made the basis for global gene pool collections. In general, the methodology for preserving collections ex situ is well developed (Börner 2006). One of the important strategies of in situ conservation is on-farm agricultural biodiversity conservation. However, there are still several concerns regarding biodiversity conservation strategies, including the correspondence between the genepools being preserved in genebanks with those grown in fields (Dulloo et al. 2010).

There are several studies comparing genetic diversity conservation strategies for crops and their wild relatives using molecular markers. Genetic diversity study from in situ and ex situ populations of Jala (*Zea mays* subsp. *mays*), using SSR markers showed little differentiation between these groups and revealed that the ex situ Jala collections contained the diversity found today in the field, even though diversity was under-represented in individual repository populations (Rice et al. 2006). While for two potato species *Solanum jamesii* and *Solanum fendleri* collected in USA in 1958 and 1978 and re-collected in 1992, RAPD markers revealed significant genetic differences between gene bank-conserved and re-collected in situ populations of these potato species that may be a source of traits of interest to breeders (del Rio et al. 1997).

The breeding potential of industrial wheat species has almost been exhausted, so breeders have begun to use landraces and endemic wheat species as new sources of alleles (Riaz et al. 2017), and Ethiopian wheat, *Triticum aethiopicum* is one of these. Vavilov et al. (1931) found this wheat species and described its peculiarities during his expedition to Ethiopia in 1927. Common wheat was found in Ethiopian fields only as an impurity. After the Ethiopian expedition, he described the endemic, purple-grained wheat as a new wheat species *T. abyssinicum* and indicated that it was mostly tetraploid (Vavilov et al. 1931). This botanical name was illegitimate, and Jakubziner (1947) later renamed the species *T. aethiopicum*. The important character of this species is the presence of purple-grained varieties (Dorofeev et al. 1979). However, its spike shape and awn type are similar to that of common wheat (Dorofeev et al. 1979; Goncharov et al. 2003). Vavilov's collection of Ethiopian wheat is still maintained at the N.I. Vavilov All-Russian Institute of Plant Genetic Resources (VIR). We now know that the species is endemic to Ethiopia and Eritrea in the north of Africa and Yemen in the south of the Arabian Peninsula. Recently, *T. aethiopicum* was also found on the south-eastern coast of the Arabian Peninsula in Oman (Al Khanjari et al. 2008) and probably in Egypt (Gowayed 2009; Filatenko and Hammer 2014). Currently, the species is only cultivated in Ethiopia and Eritrea. A large proportion of the wheat grown in Ethiopia is still this species (Teklu and Hammer 2006). Purple-grain accessions of *T. aethiopicum* are widely cultivated in the Ethiopian highlands despite the claim that they are of lower quality and fetch lower market prices than the white or red coloured grain types (Belay et al. 1995). The purple-coloured pericarp is formed in the maternal tissue due to the production of anthocyanins (Zeven 1991), which is of interest for food production (Gordeeva 2015).

The species is of current interest to plant breeders. Thus, *T. aethiopicum* has been studied intensively, especially its economically valuable traits, such as storage proteins (Letta et al. 2005) as well as some other agronomically important traits (Belay et al. 1995; Teklu and Hammer 2009), and it was used to produce the cultivars ‘Sevinge’ and ‘Jafary’ in Azerbaijan (Dorofeev et al. 1987). An increasing interest has been taken in studying the interconnection between the accumulation of anthocyanins in the pericarp of the wheat grain and the reaction of the grain to artificial ageing (Gordeeva et al. 2013), which is the characteristic that is considered valuable in Ethiopia. Earlier Ethiopian wheat was used in breeding to mark fodder grain of common wheat with purple pericarps (Gilchrist and Sorells 1982), and now *T. aethiopicum* is a popular source of antioxidants (Bartl et al. 2015), phenolics, anthocyanins and proteins (Eticha et al. 2010). Moreover, commercial cultivars of the species are characterised as being early maturing and resisting diseases and insect pests (Scott and Hollins 1977; Haile et al. 2013).

The Joint Ethiopian-Russian Expedition (JERBE) has permanently operated in Ethiopia since 1987. The main scope of the JERBE is to manage the field research of Russian academic biological institutes in Ethiopia. In 2012, three Russian research institutes, the Vavilov Institute of General Genetics RAS (Moscow), N. I. Vavilov All-Russian Institute of Plant Genetic Resources (VIR) (St. Petersburg) and Institute of Cytology and Genetics SB RAS (Novosibirsk), in close cooperation with the Ethiopian Biodiversity Institute repeated N.I. Vavilov's route of 1927 and recollected *T. aethiopicum* accessions in the same sites as Vavilov, after studying his archives.

The aim of the present study was to characterise the dynamics of the *T. aethiopicum* gene pool in accessions collected by the expedition of Vavilov in 1927 and 85 years later during the 2012 JERBE, using amplified fragment length polymorphism (AFLP) analysis, which is considered one of the most effective and cheap methods for genetic diversity analysis, and it has been used effectively for studying both the intraspecific and interspecific diversity of wheat (Colomba and Gregorini 2011; Sadigov et al. 2017).

Materials and methods

Plant material

The plant material used in the study included 140 *T. aethiopicum* accessions (shown in Online Resource 1). The 86 accessions that were collected during the expedition of N.I. Vavilov in 1927 are now maintained at the VIR. We collected a further 54 accessions in 2012 during the JERBE. The collection points of Ethiopian wheat accessions from the VIR collection were plotted on an electronic map (Fig. 1) that was used to locate the collection points using a global positioning system. During the expedition in 2012, all the points where Vavilov collected *T. aethiopicum* were visited, and plant material of Ethiopian wheat was resampled, if it was found at those points. Of the 86 collection points from the 1927 expedition, Ethiopian wheat was found at 70 locations in 2012. All collected accessions were submitted to the genebank of the Ethiopian Biodiversity Institute, where they were catalogued.

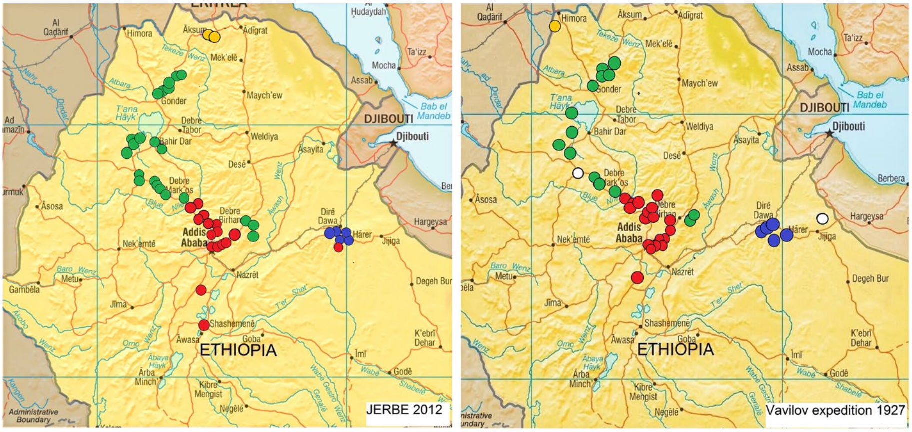

Fig. 1 Sampling locations of *T. aethiopicum* in Ethiopia. Symbols: blue circle accessions from the Hararge provinces; green circle accessions from the Amhara provinces; yellow circle accessions from the Tigrey provinces; red circle accessions from the Oromia provinces; white accessions from other provinces

Molecular analysis

Genomic DNA was isolated from 5-day-old seedlings according to the protocol of Doyle and Doyle (1987). Then AFLP analysis was performed as described by Vos et al. (1995), with minor modifications. Genomic DNA (300 ng) was digested using *EcoR*I and *Mse*I restriction endonucleases at 37 °C for 3 h. Pre-amplification was conducted with primers with a single selective nucleotide (*EcoR*I-A/*Mse*I-C), and selective amplification was conducted with primers with three selective nucleotides (*EcoR*I-ACT/*Mse*I-CCC and *EcoR*I-ACT/*Mse*I-CTA). The products were separated on 6% denatured polyacrylamide gels and stained with silver nitrate as described by Benbouza et al. (2006).

Statistical data processing

The presence/absence of amplification products on the gels were recorded visually, and the results were recorded in a binary matrix. The level of genetic differences and Nei's genetic distance were calculated using the GenAlEx 6.41 macro (Peakall and Smouse 2012). Principal coordinate analysis (PCoA) based on the Dice pairwise genetic similarity coefficient was performed using PAST 3.16. (Hammer et al. 2001). In addition, a population structure analysis was performed using the Bayes algorithm in the Structure 2.3.4 program (Pritchard et al. 2000). For the analysis, we used an admixture model, which involves mixing the genetic material, as well as correlation model, which involves the inheritance of alleles from a common ancestor through gene drift. The analysis was performed in a tenfold repetition for the number of subpopulations from k = 1 to 15, with a repetition rate of 700,000 and burn-in of 300,000. The number of true clusters in the data was estimated using the program STRUCTURE HARVESTER (Earl and von Holdt 2012).

Results

The AFLP analysis of 140 *T. aethiopicum* accessions enabled the identification of 217 fragments, and 159 (73.27%) of the detected fragments were polymorphic (see Online Resource 2). Primers *EcoR*I-ACT/*Mse*I-CCC generated 65 polymorphic fragments and primers *EcoR*I-ACT/*Mse*I-CTA produced 94 polymorphic fragments. Each of the analyzed accessions was characterized by a unique set of fragments. Of the 217 detected fragments 182 were common for JERBE and VIR accessions, while 25 fragments were detected only in VIR accessions (their frequency varied from 0.012 to 0.547) and 10 fragments were detected only in accessions collected by JERBE (their frequency did not exceed 0.093).

Shannon's index (I) and expected heterozygosity (He) were 0.265 and 0.169, respectively. The indices of genetic diversity were also determined for accessions from different collections (Table 1). The polymorphism of accessions from the VIR collection was 66.02%, He was 0.159, and I was 0.247. For accessions of Ethiopian wheat collected in 2012, these indicator values were 60.42%, 0.133 and 0.208, respectively.

The maximum Dice genetic similarity coefficient between all sampled *T. aethiopicum* accessions was between accessions K-19286/1 and K-19296/2, and the minimum value was between 19708 and K-19628 (see Table 1), and the maximum similarity coefficient value between the recently sampled accessions was between pairs of accessions 19686–19688 and 19693–19694, and the minimum value was between accessions 19681 and 19710. For the VIR accessions, the lowest coefficient value was between K-18993 and K-19569 and the highest value was the same as for the overall highest value.

The level of genetic differences between the accessions of the 1927 and 2012 collections was 17% (PhiPT = 0.169; $p < 0.010$), and Nei's genetic distance between the two collections was 0.04.

Two groups of accessions were formed in the PCoA (Fig. 2). The first group included mainly JERBE *T. aethiopicum* accessions and accessions of the 1927 collections formed the second group. The Bayesian clustering approach also showed a division into two groups corresponding to the two collection periods (Fig. 3).

The PCoA of the accessions from the two collections showed no clear division of accessions according to Ethiopian provinces (Fig. 4). The 1927 *T. aethiopicum* accessions were more evenly distributed than the 2012 accessions (Fig. 4).

Table 1 Genetic diversity parameters of the *T. aethiopicum* accessions obtained using amplified fragment length polymorphism analysis

Parameters of polymorphism	All collected accessions	Accessions from the JERBE in 2012	Accessions from the Vavilov expedition
Number of accessions	140	54	86
Percentage of polymorphism	73.27	60.42	66.02
Dice genetic similarity index (min–max/average)	0.756–0.996/0.866	0.772–0.989/0.903	0.779–0.996/0.869
Expected heterozygosity (He)	0.169	0.133	0.159
Shannon's information index (I)	0.265	0.208	0.247

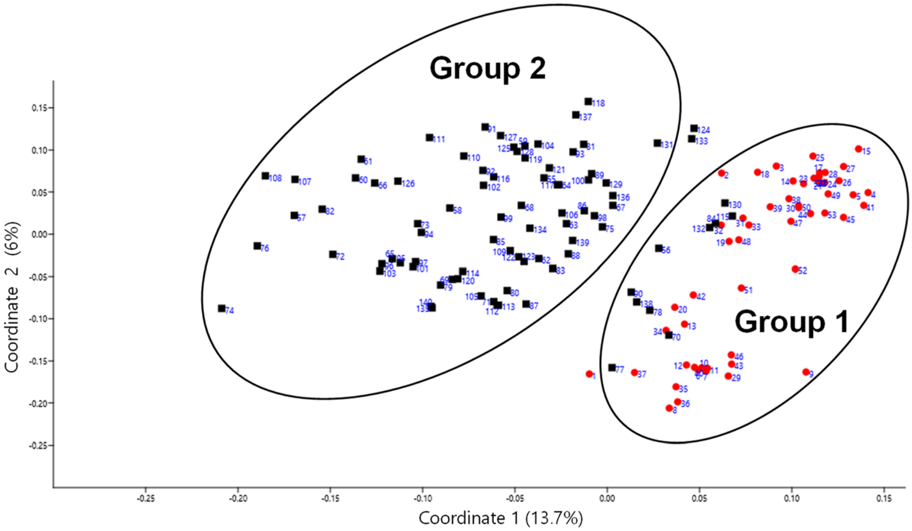

Fig. 2 Principal coordinates analysis of 140 *T. aethiopicum* accessions, based on the Dice similarity coefficient. Symbols: filled square accessions collected by Vavilov in 1927; red circle accessions collected by the Joint Ethiopian-Russian Biological Expedition in 2012. The numbers of accessions are given in accordance with Online Resource 1

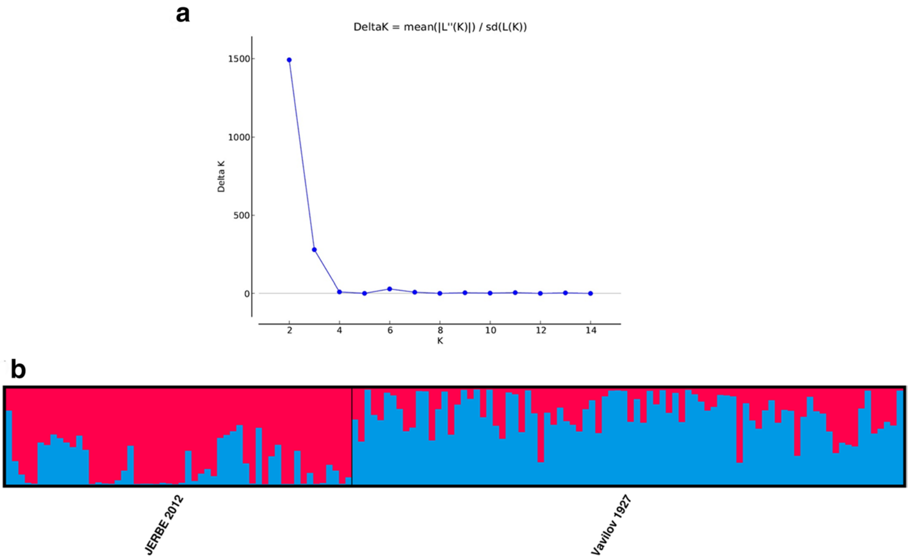

Fig. 3 **a** Estimation of the most likely number of genetic clusters (k) by the *deltaK* statistic, inferred with the Structure Harvester program; **b** Probability of assignment of *T. aethiopicum* accessions to groups, identified by the Structure 2.3.4 program, with the number of subpopulations $k=2$. Accessions on the graph are placed in order according to their numbers in Online Resource 1

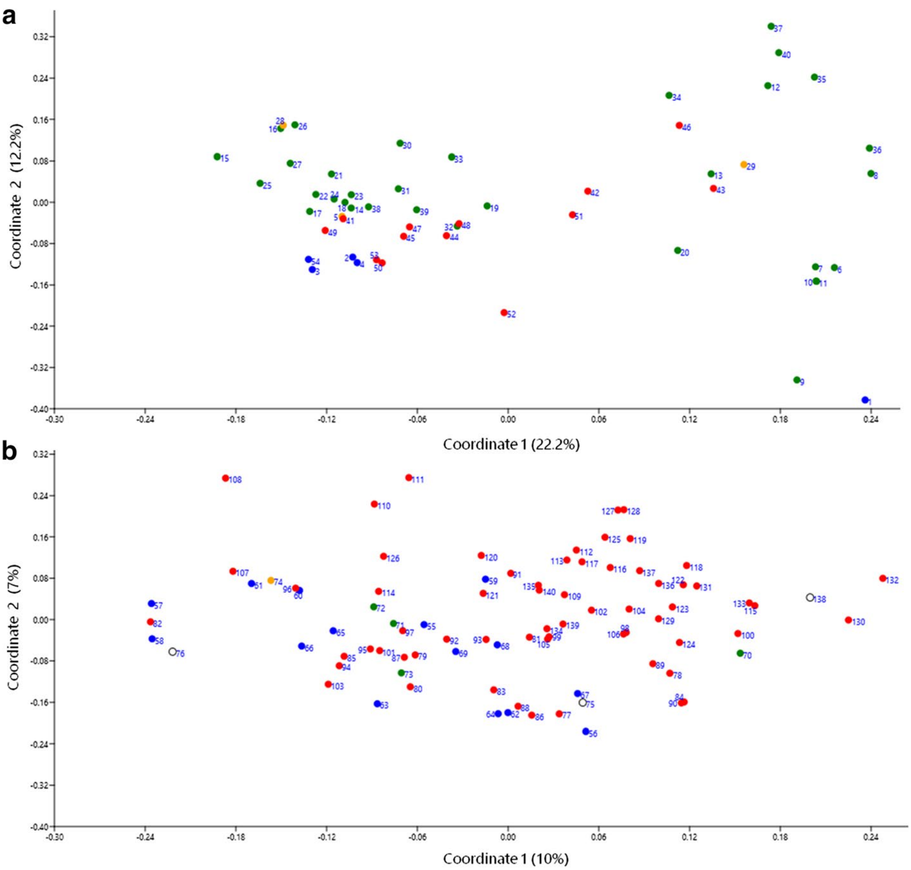

Fig. 4 Principal coordinates analysis of *T. aethiopicum* accessions from different Ethiopian provinces. **a** accessions collected by the Joint Ethiopian-Russian Biological Expedition in 2012; **b** accessions collected by Vavilov in 1927. Symbols: blue circle accessions from the Hararge provinces; green circle accessions from the Amhara provinces; yellow circle accessions from the Tigrey provinces; red circle accessions from the Oromia provinces; white circle accessions from other provinces. The accession numbers are given in accordance with Online Resource 1

Discussion

On-farm management is an important component of the general strategy for in situ plant biodiversity conservation (Maxted et al. 2002; Hammer et al. 2003). However, on-farm populations are dynamic systems, and genetic shifts can occur over time (Thomas et al. 2012). Currently, limited data exist on the temporal changes in genetic diversity that occur in farmer's fields (Thormann et al. 2018). Therefore, it is uncertain whether there is stability or loss in the genetic diversity of cultivated plants (Khlestkina et al. 2004) and whether qualitative changes in allelic composition occur over time (Thormann et al. 2017,2018).

This is difficult to study because it is hard to reassemble landraces from areas of their origin and where they were collected for the first time to conduct comparative analysis. In addition, improved varieties are often cultivated in these places, which in some cases are difficult to distinguish from local ones using morphological features.

Ethiopian wheat is an almost ideal object for studying temporal changes in the genetic structure of a crop. It has a very characteristic morphological appearance, which assists researchers in avoiding technical errors during in situ accession collecting as well as during ex situ reproduction. In addition, this wheat is only still cultivated in the Abyssinian highlands in Ethiopia, which guarantees that the population has not been changed by gene flow from other geographic regions.

It is well known that in 1927, the famous Russian scientist N.I. Vavilov conducted an expedition in Ethiopia (former Abyssinia) where he discovered and collected a huge diversity of local wheat. The results of this trip and subsequent studies of the collected accessions were described in his diaries and the books "Five continents" (Vavilov 1997) and "Abyssinian wheats" (Vavilov et al. 1931).

Archival data concerning the details of the expedition of N.I. Vavilov, which are stored in N.I. Vavilov's museum at the VIR in St. Petersburg and the Vavilov Institute of General Genetics in Moscow, allowed us to meticulously reconstruct the route of the Vavilov expedition (Fig. 5) and determine the geographical collection points of local wheat accessions (Fig. 1).

In 2012, the joint expedition of three Russian research institutes (Vavilov Institute of General Genetics RAS, N.I. Vavilov All-Russian Institute of Plant Genetic Resources (VIR) and Institute of Cytology and Genetics SB RAS) together with the Institute of Biodiversity of Ethiopia and under the umbrella of the JERBE followed this path and attempted to collect accessions in the same sites (Fig. 1).

The results of the JERBE showed that most of Vavilov's collection points still contain local tetraploid wheat, which is often in admixture with modern breeding cultivars. Local tetraploid wheat was mostly represented in farmer's fields that were far away from the main roads. Often, these fields could only be reached on foot. The highest diversity of Ethiopian

Fig. 5 Archival map with the route of the Vavilov expedition in Ethiopia

wheat was found near the cities of Gondor, Ankober and Debre Zeit. Local Ethiopian wheat appeared in fields at an altitude of 2400–2600 m above sea level (unpublished). Below this height, maize, sorghum, teff and improved varieties of common wheat prevail, and barley grows at an altitude of 2800–3000 m.

It is worth noting that *T. aethiopicum* accessions are mainly preserved by elderly farmers or in the parishes of churches, as Ethiopian wheat flour is intended for baking bread in the Eucharist sacrament, at some distance from the capital and major cities, which indicates a tendency for diversity reduction associated with changes in Ethiopian culture. It can be argued that we managed to collect enough representative material, at least in most of Vavilov's collecting sites.

According to the terms of the agreement between the JERBE and the Institute of Biodiversity of Ethiopia, all the collected material was transferred to the genebank of this Institute, where it was catalogued and deposited. It could not be deposited in other genebanks, but it could be used for scientific research in Russian laboratories. Since the accessions collected by N.I. Vavilov in 1927 and preserved in the VIR genebank were available, we were able to conduct comparative studies using genetic markers.

The first study performed, using cytogenetic markers (chromosomal C-banding), showed that there was no system change for 85 years in the polymorphism of the heterochromatic chromosomal zones or spectra of chromosomal rearrangements, as these structures remained typical for Ethiopian wheat, but the frequency of the marker chromosome variants changed and the proportion of translocations increased (Badaeva et al. 2018).

In this paper, for the first time, we present data obtained using random molecular markers (AFLP). The genetic diversity level of accessions from the VIR and 2012 collections showed comparable levels of polymorphism (60.6%) to a study of 79 *Triticum durum* accessions from Azerbaijan using AFLP analysis (Sadigov et al. 2017). The level of genetic differentiation between the two collections was not high. However, the PCoA and Bayesian clustering approach showed that the studied accessions could be divided into two groups mainly due to sampling time, which is similar to data obtained earlier by Badaeva et al. (2018) during cytogenetic analysis of tetraploid Ethiopian wheat accessions.

Badaeva et al. (2018) also showed the unevenness of the geographical distribution of the marker rearrangements. In our study, accession differentiation, according to geographical location, was not revealed. Alamerew et al. (2004) investigated the genetic diversity of 69 *T. aestivum*, 54 *T. aethiopicum* and 12 *T. durum* accessions from the Ethiopian genebank by applying 22 wheat microsatellites. They showed that the studied accessions were clustered with respect to the ploidy level, and did not group according to their geographic origins (Alamerew et al. 2004).

Thus, our results indicate two main points:

1. The level of genetic diversity in the collections that were collected by Vavilov in 1927 and our expedition in 2012 did not differ significantly (66.02% and 60.42%, respectively), as in the case of the cytogenetic analysis (Badaeva et al. 2018).

2. Our study shows that there has been a significant qualitative shift in allelic diversity in the material collected at different times at the same locations in Ethiopia. The accessions were evidently divided into two groups (Figs. 2, 3) according to collection time rather than geographical location.

Currently, it is hard to establish what evolutionary pressure caused this shift. Over the past hundred years, the climatic conditions in Ethiopia have not changed significantly, although, in the absence of reliable climate observations, this cannot be stated definitely. However, the huge variety of agro-environmental niches caused by the mountainous terrain in Ethiopia makes tracking changes in climate conditions extremely

Fig. 6 Local farmers with a plough-spear. Photo by N. P. Goncharov

difficult. The nature of the farming system has not changed either. Local farmers use the same farming techniques as their ancestors centuries ago: the plough-spear (Fig. 6) and a pair of oxen. In this regard, it is difficult to find differences between the photographs taken by Vavilov and those taken during the JERBE.

We believe that the genetic shift that we observed could be the result of artificial selection, which is on going during the reproduction of local landraces on traditional farms. An alternative explanation is that there was a change in material from the VIR collection, which was reproduced at VIR experimental stations under atypical for Ethiopian wheat climatic conditions. However, it should be noted that the accessions from the VIR collection were reproduced no more than 10 times over the past 85 years, while accessions from Ethiopia went through about 170 generations if we consider that there are two harvests per year.

The question of the influence of the internal heterogeneity of the landraces on the analysis results remains open. It is well known that almost all landraces are genetically heterogeneous (Brown 1999; Melnikova et al. 2010). However, the AFLP analysis we performed only included the genotyping of one grain from each of the collected accession, which significantly reduces the representativeness of the accession and leaves many biotypes outside the scope of this analysis. This problem could be solved by using new genotyping technologies, such as genotyping by sequencing technology together with DNA bulk analysis, and although such an approach is unlikely to lead to a fundamental change in the picture we received, it could still give results that are more accurate.

The clarification of all these issues requires additional research, but several conclusions can already be drawn. Firstly, we confirmed that ex situ and on-farm biodiversity conservation is different and they are exposed to different evolutionary pressures. Second, our findings suggest that the replenishment of ex situ collections through repeated expeditions to the previous collection sites would be beneficial. Finally, the so-called native breeding of landraces, which over the millennia of civilisation development has generated a considerable spectrum of plant cultivars and forms, which modern breeding used throughout the twentieth century and continues to use now, is still used on traditional farms. Unfortunately, the direction of this breeding is difficult to determine.

Conclusion. The level of genetic diversity in the collections of *T. aethiopicum* accessions collected by N. I. Vavilov in 1927 and the JERBE in 2012 did not differ significantly. However, it was shown that the studied accessions could be divided into two genetically distinct groups according to sampling time: accessions from Vavilov's collection, which were conserved and reproduced in the VIR, and our accessions collected 85 years later. This is possibly the result of artificial selection, which occurs on farms due to local landraces reproduction during cultivation. The second reason is a change in the material from the VIR collection, which could have occurred through reproduction under atypical growing conditions, such as through natural selection against certain alleles in heterogeneous populations. We cannot determine which of these possible factors have contributed, but this study has demonstrated that the two strategies of genetic diversity conservation, ex situ (genebank) and in situ (on-farm), have different influences on the evolution and divergence of genetic material.

Author contributions EZ, NG and AK collected accessions. AT and LD performed the AFLP analysis and statistical analysis of the obtained data. NG designed the study and performed the green house experiments. AT, NG and AK wrote the manuscript. EZ, NG and AK reviewed the manuscript. All authors have read and approved the final manuscript.

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Data availability All data generated or analysed during this study are included in this published article and its supplementary information files.

Compliance with ethical standards

Conflicts of interest The authors declare that they have no competing interests.

References

Al Khanjari S, Filatenko AA, Hammer K, Buerkert A (2008) Morphological spike diversity of Omani wheat. Genet Resour Crop Evol 55:1185–1195. https://doi.org/10.1007/s10722-008-9319-9

Alamerew S, Chebotar S, Huang X, Röder M, Börner A (2004) Genetic diversity in Ethiopian hexaploid and tetraploid wheat germplasm assessed by microsatellite markers. Genet Resour Crop Evol 51(5):559–567

Badaeva ED, Shishkina AA, Goncharov NP, Zuev EV, Lysenko NS, Mitrofanova OP et al (2018) Evolution of *Triticum aethiopicum* Jakubz. from the position of chromosome analysis. Russ J Genet 54(6):629–642. https://doi.org/10.1134/S1022795418060029

Bartl P, Albreht A, Skrt M, Tremlová B, Oštádalova M, Šmejkal K et al (2015) Anthocyanins in purple and blue wheat grains and in resulting bread: quantity, composition, and thermal stability. Int J Food Sci Nutr 66(5):514–519. https://doi.org/10.3109/09637486.2015.1056108

Belay G, Tesemma T, Bechere E, Mitiku D (1995) Natural and human selection for purple-grain tetraploid wheats in the Ethiopian highlands. Genet Resour Crop Evol 42:387–391

Benbouza H, Jacquemin J, Baudoin J, Mergeai G (2006) Optimization of a reliable, fast, cheap and sensitive silver staining method to detect SSR markers in polyacrylamide gels. Biotechnol Agron Soc Environ 10(2):77–81

Börner A (2006) Preservation of plant genetic resources in the biotechnology era. Biotechnol J 1:1393–1404. https://doi.org/10.1002/biot.200600131

Brown AHD (1999) The genetic structure of crop landraces and the challenge to conserve them *in situ* on farms. In: Brush SB (ed) Genes in the field: on-farm conservation of crop diversity, Canada. IDRC, Ottawa, pp 29–48

Colomba MS, Gregorini A (2011) Genetic diversity analysis of the durum wheat Graziella Ra, *Triticum turgidum* L. subsp. *durum* (Desf.) Husn. (Poales, Poaceae). Biodivers J 2(2):73–84

CBD (Convention on biological diversity) (1992) https://www.cbd.int/doc/legal/cbd-en.pdf. Accessed 1 Jul 2019.

Del Rio AH, Bamberg JB, Huaman Z, Salas A, Vega SE (1997) Assessing changes in the genetic diversity of potato gene banks. 2. *In situ* vs *ex situ*. Theoret Appl Genetics 95(1–2):199–204

Dorofeev VF, Filatenko AA, Migushova EF, et al (1979) Kul'turnaya flora SSSR (Cultural Flora of the Soviet Union), vol 1: Pshenitsa (Wheat). Kolos, Leningrad

Dorofeev VF, Udachin RA, Semenova LV et al (1987) Pshenitsy mira. Agropromizdat, Leningrad

Doyle JL, Doyle JJ (1987) A rapid DNA isolation procedure for small quantities of fresh leaf tissue. Phytochem Bull 19:11–15

Dulloo ME, Hunter D, Borelli T (2010) *Ex situ* and *in situ* conservation of agricultural biodiversity: major advances and research needs. Not Bot Hort Agrobot Cluj 38(2):123–135

Earl DA, von Holdt BM (2012) STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. Conserv Genetics Resourc 4(2):359–361. https://doi.org/10.1007/s12686-011-9548-7

Eticha F, Grausgruber H, Berghoffer E (2010) Multivariate analysis of agronomic and quality traits of hull-less spring barley (*Hordeum vulgare* L.). J Plant Breed Crop Sci 2(5):81–95

Filatenko AA, Hammer K (2014) Wheat landraces from Oman: a botanical analysis. Emir J Food Agric 26(2):119–136. https://doi.org/10.9755/ejfa.v26i2.16760

Flyaksberger KA (1939) *Triticum* L. pr.p. Wheat. In: Identification of real bread (Wheat, rye, barley, oats), M-L.:GIZ kolh. isovh. lit-ry, Moscow, pp 11–236 (In Russian)

Fu YB, Peterson GW, Scoles G, Rossnagel B, Schoen DJ, Richards KW (2003) Allelic diversity changes in 96 Canadian oat cultivars released from 1886 to 2001. Crop Sci 43(6):1989–1995. https://doi.org/10.2135/cropsci2003.1989

Gao L, Chen W, Jiang W, Ge S, Hong D, Wang X (2000) Genetic erosion in northern marginal population of the common wild rice *Oryza rufipogon* Griff. and its conservation, revealed by the change of population genetic structure. Hereditas 133:47–53. https://doi.org/10.1111/j.1601-5223.2000.00047.x

Gilchrist JA, Sorells ME (1982) Inheritance of kernel color in "charcoal" wheat. J Heredity 73:457–460

Goncharov NP, Mitina RL, Anfilova NA (2003) Inheritance of awnlessness in tetraploid wheat species. Russ J Genet 39:463–466. https://doi.org/10.1023/A:1023326202320

Gordeeva EI (2015) Genetic regulation of purple color of the soft wheat (*Triticum aesticum* L.) pericarp. Dissertation, Instituty of Citology and Genetis, Siberian Branch of Russian Academy of Science, Novosibirsk

Gordeeva EI, Khlestkina EK (2013) The relationship between the accumulation of anthocyanins in the pericarp of the wheat grain and the reaction to artificial aging in seeds. In: Butakov VV, Kandalinceva NV, Prosenko AE (eds) Free radicals and antioxidants in chemistry, biology, and medicine: materials of the scientific and practical conference, part 1. NGPU, Novosibirsk, p 63

Gowayed S (2009) Egyptian wheat. Dissertation, Kassel University Cuvillier-Verlag, Göttingen (cited in Filatenko, Hammer, 2014)

Haile JK, Hammer K, Badebo A, Singh RP, Röder MS (2013) Haplotype analysis of molecular markers linked to stem rust resistance genes in Ethiopian improved durum wheat varieties and tetraploid wheat landraces. Genet Resour Crop Evol 60:853–864. https://doi.org/10.1007/s10722-012-9880-0

Halewood M (2013) What kind of goods are plant genetic resources for food and agriculture? Towards the identification and development of a new global commons. Int J Commons 7:278–312

Hammer O, Harper DAT, Ryan PD (2001) PAST: paleontological statistics software package for education and data analysis. Palaeontol Electron 4(1):1–9

Hammer K, Gladis Th, Diederichsen A (2003) *In situ* and on-farm management of plant genetic resources. Eur J Agron 19(4):509–517. https://doi.org/10.1016/S1161-0301(02)00184-3

Jakubziner MM (1947) *Triticum aethiopicum*. Selekc I Semenov 14(5):46

Khlestkina EK, Huang XQ, Quenum FJB, Chebotar S, Röder MS, Börner A (2004) Genetic diversity in cultivated plants—loss or stability? Theor Appl Genet 108(8):1466–1472. https://doi.org/10.1007/s00122-003-1572-x

Khlestkina EK, Varshney RK, Röder MS, Graner A, Börner A (2006) A comparative assessment of genetic diversity in cultivated barley collected in different decades of the last century in Austria, Albania and India by using genomic and genic simple sequence repeat (SSR) markers. Plant Genetic Re-sources 4(2):125–133. https://doi.org/10.1079/PGR2006109

Letta T, Gezu G, Kudryavtsev A, Chiapparino E, D'Egidio MG (2005) Genetic diversity of Ethiopian durum wheat varieties based on gliadin alleles. J Genetics Breed (Italy) 59(3):277–283

Maxted N, Guarino L, Myer L, Chiwona EA (2002) Towards a methodology for on-farm conservation of plant genetic resources. Genet Resour Crop Evol 49(1):31–46

Maxted N, Dulloo E, Ford-Lloyd BV, Iriondo JM, Jarvis A (2008) Gap analysis: a tool for complementary genetic conservation assessment. Divers Distrib 14:1018–1030. https://doi.org/10.1111/j.1472-4642.2008.00512.x

Melnikova N, Ganeva G, Popova Z, Landjeva S, Kudryavtsev A (2010) Gliadins of Bulgarian durum wheat (*Triticum durum* Desf.) landraces: genetic diversity and geographical distribution. Genet Resour Crop Evol 57:587–595. https://doi.org/10.1007/s10722-009-9497-0

Metakovsky E, Melnik VA, Pascual L, Wrigley CW (2019) Gliadin genotypes worldwide for spring wheats (*Triticum aestivum* L.) Genetic diversity and grain-quality gliadin alleles during the 20th century. J Cereal Sci 87:172–177. https://doi.org/10.1016/j.jcs.2019.03.008

Peakall R, Smouse PE (2012) GenALEx 6.5: genetic analysis in excel. Population genetic software for teaching and research-an update. Bioinformatics 28(19):2537–2539. https://doi.org/10.1093/bioinformatics/bts460

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155(2):945–959

Riaz A, Hathorn A, Dinglasan E, Ziems L, Richard C, Singh D et al (2017) Into the vault of the Vavilov wheats: old diversity for new alleles. Genet Resour Crop Evol 64:531–544. https://doi.org/10.1007/s10722-016-0380-5

Rice EB, Smith ME, Mitchell SE, Kresovich S (2006) Conservation and change: a comparison of *in situ* and *ex situ* conservation of Jala maize germplasm. Crop Sci 46(1):428–436. https://doi.org/10.2135/cropsci2005.06-0116

Sadigov GB, Trifonova AA, Kudryavtsev AM (2017) Genetic diversity in collection of cultivars and varieties of *Triticum durum* Desf from Azerbaijan. Russ J Genet 53(5):576–586. https://doi.org/10.1134/S1022795417050088

Scott PR, Hollins TW (1977) Interactions between cultivars of wheat and isolates of *Cercosporella herpotrichoides* Trans. Br Mycol Soc 69(3):397–403. https://doi.org/10.1016/S0007-1536(77)80077-6

Teklu Y, Hammer K (2006) Farmers' perception and genetic erosion of tetraploid wheat landraces in Ethiopia. Genet Resour Crop Evol 53:1099–1113

Teklu Y, Hammer K (2009) Diversity of Ethiopian tetraploid wheat germplasm: breeding opportunities for improving grain yield potential and quality traits. Plant Genet Resour 7(1):1–8. https://doi.org/10.1017/S1479262108994223

Thomas M, Demeulenaere E, Dawson JC, Khan AR, Galic N, Jouanne-Pin S et al (2012) On-farm dynamic management of genetic diversity: the impact of seed diffusions and seed saving practices on a population-variety of bread wheat. Evol Appl 5(8):779–795. https://doi.org/10.1111/j.1752-4571.2012.00257.x

Thormann I, Reeves P, Thumm S, Reilly A, Engels JMM, Biradar CM et al (2017) Genotypic and phenotypic changes in wild barley (*Hordeum vulgare* subsp. *spontaneum*) during a period of climate change in Jordan. Genet Resour Crop Evol 64(6):1295–1312. https://doi.org/10.1007/s10722-016-0437-5

Thormann I, Reeves P, Thumm S, Reilly A, Engels JMM, Biradar CM et al (2018) Changes in barley (*Hordeum vulgare* L. subsp vulgare) genetic diversity and structure in Jordan over a period of 31 years. Plant Genetic Resourses 16(2):112–126. https://doi.org/10.1017/S1479262117000028

van de Wouw M, Kik C, van Hintum T, van Treuren R, Visser B (2009) Genetic erosion in crops: concept, research results and challenges. Plant Genetic Resour 8(1):1–15. https://doi.org/10.1017/S1479262109990062

Vavilov NI (1997) Five continents. IPGRI/VIR, Rome. (Translated into English by Doris Löve).

Vavilov NI, Fortunatova OK, Yakubtsiner MM, Pal'mova EF, Nikolaenko EI, Stoletova EA et al (1931) The wheats of Abyssinia and their position in the general system of wheats. Bull Apl Bot Gen i sel 51:236

Vos P, Hogers R, Bleeker M, Reijans M, Van de Lee T et al (1995) AFLP: a new technique for DNA fingerprinting. Nucleic Acids Res 23:4407–4414

Zeven AC (1991) Wheats with purple and blue grains: a review. Euphytica 56:243–258

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