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Review Article

Teff (*Eragrostis tef* (Zucc.) Trotter) Breeding Progress: A Journey From the Category of Orphan Crop to a Modern Genomic Era

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Abstract

Ethiopia is both the origin and center of diversity for teff (Eragrostis tef (Zucc.) Trotter) and many other crops due to its diverse agro-ecology and culture. Teff is an autogamous and allotetraploid crop with a chromosome number of 2n=4x=40 and a staple food crop for more than 70 million people in Ethiopia. It occupies over three million hectares of land and is cultivated by over 7.2 million households. However, the yield of teff is very low as compared to other cereals cultivated in Ethiopia. Its productivity is constrained by many factors, which still need further research to intervene. Scientific teff research in Ethiopia started in the 1950s, and many improved teff varieties (about 54 until 2022) have been released to the farming community through conventional breeding approaches like pure line/mass selection and hybridization. Nowadays, the Debre Zeit (Bishoftu) Agricultural Research Center has a full mandate at the national level in teff breeding activities. Globally, only a few cereal crops are feeding the world population and getting more attention from the international scientific community; however, orphan crops like teff have recently gotten consideration from many national and international organizations due to their golden merits and nutritional quality, like gluten-free products. Many efforts have been made to improve and tackle teff breeding challenges through the molecular breeding approach, and there are some achievements. However, the major challenges of teff breeding still need focus and significant contributions from the national and international scientific communities, companies, governments, and other stakeholders. The development of gene editing tools like CRISPR/Cas9 has revolutionized and enhanced breeding in many other cereals. The application of these gene-editing tools in the teff breeding program, particularly for the challenging traits like lodging, seed size, grain yield, and other related traits, will be the next assignment for the teff breeders.

Keywords

Teff, Orphan Crops, Conventional, Molecular, Achievements, Challenges

1. Introduction

Teff (*Eragrostis tef* (Zucc.) Trotter), known as the autogamous annual grass, is native to Ethiopia and is stable cereal crop in the Ethiopian diet [1]. In Ethiopia, teff is one of the most important and preferable staple cereal crops, including in the Horn of Africa. In Ethiopia alone, it takes more than three million hectares of land (about 24.11% of the 81.46% of land dedicated to cereal crops). In terms of area coverage, it ranks first (24.11%), followed by maize (17.68%), sorghum

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(14.21%), and wheat (13.91%). Among cereals grown in Ethiopia, teff ranks second (after maize) and last (8^{th}) in terms of production (about 5.7 million tons) and productivity (around 1.85 tons/ha) among the cereals grown in Ethiopia, respectively. In Ethiopia alone, more than 70 million Ethiopians (more than half of the total population of the country) depend on teff as their main staple grain [2], and more than 7.2 million households cultivate teff [3].

Globally, a few numbers of cereal crops, like rice, wheat, and maize, are feeding the world's population. These major cereals provide over 42% of calories consumed by the whole human population [4]. However, the production of these few major cereals alone cannot satisfy the demand for food. This is because these crops are less suited to less input and poorly adapted to climate change [5, 6]. On the other hand, reliance only on these few cereal crops results in dietary imbalance and unfavorable food shortages. For this reason, diversifying food supplies by using underutilized orphan crops like teff is becoming more popular as a solution to these issues [7, 8]. Furthermore, teff is becoming more and more well-known throughout the world because it is gluten-free and has a balanced amount of important amino acids in comparison to other major cereals like rice, wheat, and maize. For example, teff is rich in starch but has a somewhat lower energy content than other cereals, which is beneficial for people with type II diabetes; that means it releases energy slowly. It also has the maximum amount of lysine and other necessary amino acids. Additionally, it has a lot of fiber, polyunsaturated fats, and is high in iron, calcium, and zinc, which are beneficial micronutrients [9, 10]. Additionally, teff fits the criteria for sustainable diets, which include being nutritionally adequate, safe, and healthy while optimizing natural and human resources. Due to its outstanding nutritional profile, teff is known as 'supergrain' and a healthy crop of our century, a stable grain, climate smart, and highly preferred by both consumers and producers [12].

Nowadays, teff is becoming more popular in the United States of America for animal feed (forage) due to its desirable traits like drought tolerance and rapid growth habit [13]. As compared to major cereals like maize, wheat, and rice, underutilized/orphan crops like teff are among the most nutritious grains and are more resilient to marginal soil and climate conditions. For instance, in Ethiopia, about 10% of arable (cultivable) land is under the influence of waterlogging; however, teff can germinate in these waterlogged soils and establish seedlings on which other crops may fail to germinate; that is why teff is called a crop of choice [14]. Several authors have suggested that orphan crops will help to implement the UN Sustainable Development Goals in low-income countries like Africa, Asia, and Latin America, including developed Western countries' demand for new, healthier foods [6, 15-17]. Among the UN Sustainable Development Goals, no poverty, zero hunger, and good health and wellbeing are some of them. These goals can be ensured if crops like teff, endowed with a potential to withstand different environmental stresses, are well utilized [11]. Different reports are indicating that by the coming 2050, the world population will reach 9.8 billion. In addition to population growth, issues such as pandemics, conflicts, socio-economic disparities, competition for food and biofuel for available land resources, and climate change are also exacerbating food security. Because underutilized or "orphan" crops have the benefit of already being well integrated into the socioeconomics of the area, their use is crucial to ensuring food security [17-19]. Due to their greater stability in the face of frequently shifting demand and environmental conditions, orphan crops like teff are also the crops that farmers and consumers prefer [20], and teff is serving as a source of forage to feed animals in many parts of the world, such as the Mediterranean [21]. In line with this, the majority of Ethiopian farmers grow teff because of its exceptional golden traits, such as its ability to adapt to changing weather patterns, produce revenue for households, and meet nutritional needs. It is also a versatile/multipurpose crop, with its grain used for human consumption (especially to form the popular pancake-like bread known as "*Injera*") and its straws used for plastering local homes after mixing with mud and feeding livestock [1]. However, due to the changing demands and numerous difficulties faced by Ethiopia's small-scale-farmers, the need to conserve, characterize, and use the current teff genetic variety should be taken into consideration [22], and for the genetic improvement of a crop and climate study, inclusion of traditional knowledge is important [23].

A number of efforts have been conducted in the fields of molecular and biotechnology to improve teff and tackle the challenging traits. However, because of the crops' nature, there have been numerous obstacles during this time, such as the small size of the seeds, crossing difficulties, shattering, lodging, less focus, mechanization issues, and capacity building [24]. Molecular markers have been instrumental in identifying the characteristics of the genes causing the dwarfed phenotype in other cereals, such as rice and wheat, that revolutionized the Green Revolution [25], as well as in facilitating the selection and identification of the desired phenotype [26]. However, in teff, sufficient scientific information is not generated about dwarfing genes, even though attempts to clone and sequence the orthologues of the rht1 (reduced height) and sd1 (semi-dwarf) genes are in progress [27, 28]. However, to some extent, there is a possibility to improve lodging problems in teff through conventional breeding due to the existence of plenty of genetic variation for traits like plant height, culm diameter, and tillering capacity via indirect selection for these traits [29]. A genome-wide association study was conducted in order to identify loci and candidate genes for traits like yield, local adaptation, farmers' appreciation, and phenology. Accordingly, the results of the study revealed areas around Tana lake are vulnerable to climate change, and teff landraces (farmers' varieties) should be utilized to build resilience climate scenarios [23], and a strong association between grain yield, lodging, and days to heading was reported [30]. Agronomic practices like sowing rate can also reduce lodging [31]. The Ethiopian farmers are cultivating teff despite many difficulties and fewer research achievements in teff because of the following merits over other cereal crops: I) Adaptability to a variety of agro-ecological conditions (0-3000 m. a. s. l.), including conditions that are marginal for the majority of other crops. II) Resilience to drought and waterlogging conditions. III) Suitability for a wider range of cropping systems and crop rotation schemes. IV) Use as a catch crop and low-risk, dependable crop, particularly as a replacement crop when long-season crops (like maize and sorghum) fail due to drought, pests, and/or other disasters. V) Relative healthiness of the crop in the field and storage because it faces minimal or no significant threats from disease and pest epidemics [14, 20].

The recent discovery of genomes and candidate genes particularly that offer synthenic comparisons for the evolution of C4 photosynthesis has made a significant contribution to the study of orphan/underutilized cereal and legume crops. This helps to enhance important attributes such as drought resistance, photorespiration efficiency, and nutritional qualities. To use this finding in a breeding program, more research is still required [32]. Therefore, this paper reviews an overview of teff breeding progress, a journey from the category of orphan crop to a modern genomic era, and forecasts future perspectives in the teff breeding program.

2. Origin and Taxonomy of Teff

Ethiopia is the origin and diversity center for teff [(*Eragrostis tef* (Zucc.) Trotter] and many other important oil crops, such as noug (*Guizotia abyssinica* (L. f.) Cass.), Ethiopian mustard or gomenzer (*Brassica carinata* A. Braun), and horticultural crops, such as enset (*Enset ventricosum* (Welw.) Cheeseman), coffee (*Coffea arabica* L.), and anchote (*Coccinia abyssinica* (Lam.) Cogn) due to its diverse agro-ecology and culture [33]. Teff belongs to the grass family, *Poaceae* (formerly *Gramineae*), subfamily *Chloridoide* (*Eragrostoidae*), tribe *Eragrostidae*, subtribe *Eragrosteae* and genus *Eragrostis*. Different nomenclature names were given to teff at different times as indicated in Table 1. However, the name, teff (*i.e.*, *Eragrostis tef* (Zucc.) Trotter), which is based on the specific epithet 'tef' previously used by Zuccagni, was proposed by Trotter in 1918, and it is the most accepted binomial nomenclature [34].

2.1. Domestication and Global Distribution of Teff

The largest genera in the grass family is Eragrostis, with over 350 species. It is believed that the pre-Semitic people who invaded northern Ethiopia domesticated teff between 4000 and 1000 B. C. The exact date and location of teff domestication, however, are still in doubt [35]. At continental level, Africa shares the largest percentage among of the Eragrostis species, which is about 43%, followed by South America (18%), Asia (12%), Australia (10%), Central America (9%), North America (6%), and Europe (2%), respectively. Teff and its wild relatives are also found in other regions of the world. Only 14 (26%) of the approximately 54 species of Eragrostis found in Ethiopia are indigenous. With a chromosomal number of 2n=4x=40, it is an allotetraploid crop that may have descended from Eragrostis pilosa. The only species in the *Chloridoidae* subfamily that are grown as cereal crops for human consumption are teff and finger millet [1, 14, 36].

Table 1. *Binomial nomenclatures given to teff by various authors at different times (Compiled from [35, 37]).*

Suggested name	Year
Poa tef Zuccagni	1775
Poa abyssinica Jacquin	1781
Poa cerealis Salisb	1796
Cynodon abyssinicus (Jacq.) Rasp.	1827
Eragrostis abyssinica (Jacq.) Link	1827
Eragrostis pilosa (L.) P. Beauv. subsp. abyssinica (Jacq.) Aschers and Graben	1900
Eragrostis tef (Zucc.) Trotter	1918
Eragrostis pilosa (L.) P. Beauv. var tef (Zucc.)	1923

2.2. Phases of Teff Breeding

The overall teff breeding phases up to date are summarized in Table 2.

Table 2. *Teff breeding phases and their respective activities.*

Phases of teff breeding	Year	Activities
Phase I	1956-1974	The first phase was mainly focused on three major activities: I) Germplasm enhancement through collection/acquisition, characterization and evaluation, systematics and conservation II) Genetic improvement: This part entirely depends on mass or pure line selection from the existing germplasm

Phases of teff breeding	Year	Activities
		III) Initiation of induced mutation using X-ray radiation was started to enhance genetic variation
Phase II	1975-1995	This phase is known as breakthrough phase in teff breeding history due the discovery of *chasmogamous* floral opening behavior of teff discovered by Tareke (1975). The opening time of teff flower was from 6:45-7:30 AM. Additionally, intraspecific hybridization was incorporated in the teff breeding program because the discovery of teff floral opening time opens an opportunity of exercising crossing technique
Phase III	1995-1998	In this phase, molecular approach breeding was started; for instance, I) Molecular markers and genetic linkage map was developed, II) Molecular genetic diversity study was started
Phase IV	1998-2003	In this phase, tissue culture technique was employed; for instance, invitro culture and interspecific hybridization, and re-appraisal of induced mutagenesis was started to solve problems of lodging and leaf rust disease
Phase V	2003-date	This phase incorporates participatory breeding approach, extensive molecular studies or genomic research approaches

2.3. Teff Variety Development Approaches

2.3.1. Conventional/Traditional Breeding Approach

The year 1974 was recorded as a breakthrough period in teff breeding history that permitted the classical teff-crossbreeding program to begin. This is due to the discovery of the opening and pollination period of teff florets that occurs early in the morning between 6:00 and 6:45 a. m. This discovery paves a great opportunity for many authors to assess teff accessions for different important traits such as lodging resistance, shattering, seed size, and leaf rust disease resistance through a conventional approach. The existence of ample genetic variations is crucial for the improvement of traits, and the assessed accessions in teff are lacking adequate genetic variation for all traits studied [1]. On the other side, the number of teff accessions found at the Ethiopian Institute of Biodiversity (EIB) has increased from 1067 to 5167. For any plant-breeding program, searching for genetic variability and germplasm enhancement is fundamental and a prerequisite activity in developing improved varieties [38]. This can be achieved through (i) the collection/acquisition, characterization, evaluation, and conservation of germplasm; (ii) hybridization (intra- and interspecific) among selected parents; and (iii) other techniques like induced mutation and marker-assisted breeding (MAB) [1, 20]. Accordingly, to enhance genetic variation in teff, the following approaches are employed in the teff breeding program: i) Indigenous germplasm: The indigenous germplasm constitutes the major source of variability for teff because teff, being a native and unique crop to Ethiopia, has rare opportunities for introductions of teff germplasm and breeding materials from abroad. ii) Hybridization: This involves mainly intraspecific crosses and recently some interspecific crossings, especially with *E. pilosa*, which is the closest relative and wild progenitor to teff.

Briefly, teff research activities started in the late 1950s; it was first bred using the conventional approach [34]. Accordingly, teff breeding improvement activity was started at the then Jimma Agricultural and Technical High School and later moved to the Debre Zeit (Bishoftu) Agricultural Research Center (DZARC) under the Ethiopian Institute of Agricultural Research (EIAR). The Debre Zeit (Bishoftu) Agricultural Research Center took the mandate to coordinate the national teff improvement program. In addition, foreign funding organizations have supported this research program, and many activities have been done [39]. This enabled both federal and regional agricultural research centers to release 54 improved teff varieties until 2021, and out of these, 28 varieties were from the Debre Zeit (Bishoftu) Agricultural Research Center (DZARC), 7 from Sirinka research center, 8 from Adet research center, 5 from Bako research center, 2 from Holeta research center, 2 from Areka research center, 1 from Axum, and 1 from Melkasa research centers. These efforts have shifted the yield plateau from below 1 ton/ha at the beginning of the second millennium to 1.85 tons/ha in 2018 [3, 14].

There are some varieties of teff developed through a conventional approach and the best performer. For instance, the *Quncho* (*974 × 196)-HT ̗387 (RIL355*) variety was developed from the cross between two old varieties, namely Magna (DZ-01-196), characterized by a very white seed color but low in yield, and Dukem (DZ-01-974), characterized by pale white seed color (not preferred by producers/farmers) but high in yield, and the Felagot (DZ-Cr-442/RIL-77C) variety was developed from *Quncho* (the popular variety) and *Gea Lammie* (local cultivar). This indicates that conventional teff breeding through participatory variety selection (PVS) and participatory plant breeding (PPB) are promising in developing better varieties to improve different traits of interest. Among the 54 teff improved varieties released to the farming community up to 2022, about 52% were developed through hybridization, while the remaining 48% were via pure line/mass selection from the local cultivars (farmers' variety). From the released teff varieties, *Quncho*, *Kora*, *Magna*, *Enatite*, *Dagim*, and *Dukem* are for optimum rainfall areas, while the relatively early maturing varieties like *Boset*, *Tsedey*, and *Simada* are meant for terminal drought-prone areas [14]. Enhancement of genetic variation is compulsory to improve traits of interest. There is mechanism used to enhance genetic variation in teff such as the use of a) indigenous germplasm through collection, evaluation, characterization, and conservation, b) hybridization (intra and inter-specific hybridization and c) induced mutation [1].

Recently, seven improved varieties of teff were released (from 2017 to 2022) enhanced with different desirable traits. Tesfa (2017) enhanced with lodging resistance, Eba (2019) enhanced with high yield, Bora (2019) enhanced with drought tolerance, Boni (2021) enhanced with drought tolerance, Bishoftu (2021) enhanced with early maturity, Kulle (2022) enhanced with late maturity and high yield, and Bereket (2022) enhanced with late maturity and high yield [40]. The details of other released teff varieties are shown in Table 3.

Table 3. *Improved teff varieties released in Ethiopia for different environmental conditions until 2022.*

№	Name		Variety release					Grain yield t ha-1	
	Common name	Variety name	Year	Center	Breeding method	Days to mature	Seed color	Research field	On-farm
Varieties for optimum rainfall areas									
1	Asgori	DZ-01-99	1970	DZ	Selection	80-130	Brown	2.2-2.8	1.7-2.2
2	Magna	DZ-01-196	1970	DZ	Selection	80-113	Very white	1.8-2.2	1.4-1.6
3	Enatite	DZ-01-354	1970	DZ	Selection	85-130	Pale white	2.2-3.0	1.7-2.2
4	Wellenkom	DZ-01-787	1978	DZ	Selection	90-130	Pale white	2.2-3.0	1.7-2.2
5	Menagesha	DZ-Cr-44	1982	DZ	Hybridization	125-140	White	2.2-2.8	1.7-2.2
6	Melko	DZ-Cr-82	1982	DZ	Hybridization	112-119	White	2.2-3.0	1.8-2.2
7	Gibe	DZ-Cr-255	1993	DZ	Hybridization	114-126	White	2.0-3.0	1.6-2.2
8	Dukam	DZ-01-974	1995	DZ	Selection	76-138	White	2.4-3.4	2.0-2.5
9	Ziquala	DZ-Cr-358	1995	DZ	Hybridization	75-137	White	2.1-3.4	1.8-2.4
10	Holeta Key	DZ-01-2053	1998	Holeta	Selection	124-140	Brown	2.1-3.4	1.8-2.5
11	AmboToke	DZ-01-1278	1999	Holeta	Selection	125-140	White	2.1-3.4	1.9-2.6
12	Koye	DZ-01-1285	2002	DZ	Selection	104-118	White	2.1-3.4	1.8-2.5
13	Ajora	PGRC/E205396	2004	Areka	Selection	85-110	White	1.8-2.2	1.5-1.7
14	Yilmana	DZ-01-1868	2005	Adet	Selection	98-118	White	1.6-3.0	1.4-2.1
15	Dima	DZ-01-2423	2005	Adet	Selection	94-116	Brown	1.6-3.2	1.4-2.2
16	Quncho	DZ-Cr-387 RIL355	2006	DZ	Hybridization	80-113	Very white	2.2-2.8	2.0-2.2
17	Guduru	DZ-01-1880	2006	Bako	Selection	110-132	White	1.5-2.3	1.4-2.0
18	Kena	23-Tafi-Adi-72	2008	Bako	Selection	110-134	Very white	1.7-2.7	1.3-2.3
19	Etsub	DZ-01-3186	2008	Adet	Selection	92-127	White	1.9-2.7	1.6-2.2
20	Kora	DZ-Cr-438 RIL133B	2014	DZ	Hybridization	110-117	Very white	2.3-2.8	2.0-2.3
21	Werekiyu	Acc. 214746A	2014	Sirinka	Selection	90-100	White	2.0-2.7	1.8-2.2
22	Abola	DZ-Cr-438 RIL7	2015	Adet	Hybridization	112-115	Very white	2.1-2.7	1.8-2.3
23	Dagim	DZ-Cr-438 RIL91A	2016	DZ	Hybridization	116-144	Very white	2.4-3.1	2.0-2.5
24	Negus	DZ-Cr-429 RIL125	2017	DZ	Hybridization	112-116	Very white	2.4-3.1	2.1-2.6
25	Felagot	DZ-Cr-442 RIL77C	2017	DZ	Hybridization	108-112	Brown	2.2-2.8	1.9-2.4
26	Tesfa	DZ-Cr-457 RIL181	2017	DZ	Hybridization	112-120	White	2.3-3.0	2.1-2.7

№	Name		Variety release					Grain yield t ha-1	
	Common name	Variety name	Year	Center	Breeding method	Days to mature	Seed color	Research field	On-farm
Varieties for optimum rainfall areas									
27	Heber-1	DZ-Cr-419	2017	Adet	Hybridization	93-114	White	2.0-2.7	1.7-2.2
28	Areka-1	DZ-Cr-401	2017	Areka	Hybridization	112-119	White	1.8-2.2	1.4-1.7
29	Abay	Acc # 225931	2018	Adet	Selection	95-132	White	2.4-3.0	1.8-2.2
30	Dursi	ACC.236952	2018	Bako	Selection	100-125	White	2.1-2.5	1.9-2.2
31	Jitu	DZ-01-256	2019	Bako	Selection	100-125	White	2.1-2.5	1.9-2.4
32	Ebba	DZ-Cr-458 RIL18	2019	DZ	Hybridization	95-110	Very white	2.3-3.0	2.0-2.6
33	Washera	DZ-Cr-429 RIL 29	2019	Adet	Hybridization	108-125	Very white	2.3-3.2	2.0-2.5
34	Bishoftu	DZ-Cr-497 RIL133	2020	DZ	Hybridization	94-110	Very white	2.4-3.2	2.0-2.8
35	Axumawit	DZ-Cr-429 RIL 7	2020	Axum	Hybridization	100-126	Pale white	1.7-2.2	2.1-2.6
36	Jarso	-	2021	Bako	Hybridization	-	-	-	-
37	Takusa	DZ-Cr-459 RIL104	2021	Adet	Hybridization	93-113	White	1.9-2.6	1.7-2.1
Varieties for low rain fall (terminal drought-prone) areas									
38	Tsedey	DZ-Cr-37	1984	DZ	Hybridization	82-90	White	1.8-2.8	1.4-1.9
39	Gola	DZ-01-2054	2001	Sirinka	Selection	77-90	White	2.0-2.4	1.6-2.0
40	Gerado	DZ-01-1281	2002	DZ	Selection	82-87	White	2.0-2.4	1.6-2.0
41	Key Tena	DZ-01-1681	2002	DZ	Selection	84-93	Deep Brown	2.0-2.5	1.6-1.9
42	Zobel	DZ-01-1821	2005	Sirinka	Selection	78-85	White	2.0-2.5	1.5-2.1
43	Genete	DZ-01-146	2005	Sirinka	Selection	78-85	Pale white	1.8-2.4	1.6-2.1
44	Amarach	HO-Cr-136	2006	DZ	Hybridization	63-87	White	1.8-2.5	1.4-2.2
45	Mechare	Acc. 205953	2007	Sirinka	Selection	79-90	Pale white	1.8-2.5	1.4-2.2
46	Gemechis	DZ-Cr-387 RIL127	2007	Melkassa	Hybridization	62-85	White	1.7-2.6	1.5-2.2
47	Simada	DZ-Cr-385 RIL295	2009	DZ	Hybridization	72-88	White	2.0-2.8	1.6-2.4
48	Lakech	DZ-Cr-387 RIL273	2009	Sirinka	Hybridization	74-85	Very white	2.2-2.7	1.7-2.4
49	Boset	DZ-Cr-409	2012	DZ	Hybridization	75-90	Very white	1.9-2.8	1.8-2.2
50	Bora	DZ-Cr-453 RIL120B	2019	DZ	Hybridization	74-85	Very white	2.0-2.8	1.8-2.4
51	Mena	DZ Cr- 428	2019	Sirinka	Hybridization	80-86	Very white	2.2-2.8	2.0-2.5
52	Boni	DZ-Cr-498 RIL 37	2021	DZ	Hybridization	80-90	Very white	2.0-3.8	1.8-2.6
Varieties for highland (water logged) areas									
53	Gimbichu	DZ-01-899	2005	DZ	Selection	118-137	White	1.5-2.2	1.4-2.0
54	DegaTef	DZ-01-2675	2005	DZ	Selection	112-123	White	1.5-2.4	1.4-2.2

DZ= Debre Zeit; Compiled from [24, 40]

2.3.2. Molecular Breeding Approach

The application of molecular marker technology in teff breeding is still in its infancy and is a relatively new development (in the third phase of teff breeding milestones) in comparison to conventional breeding [24]. To complement and accelerate conventional teff breeding, however, there have been substantial and ongoing attempts to build the pre-requisites for the application of molecular approaches and biotechnological technologies [1]. These authors discussed the molecular breeding methods for developing teff varieties as follows: (1) developing molecular markers; (2) analyzing genetic diversity and relationships at the molecular level; (3) creating molecular marker linkage maps; (4) identifying quantitative trait loci (QTL); (5) regeneration and transformation techniques; and (vi) high-throughput methods like eco-TILLING and Targeting Induced Local Lesion IN Genomes (TILLING). Nowadays, there are more than 1500 locus-specific teff markers, which can be used in genetic studies [14], and utilization of underutilized crops using genomic selection and speed breeding is compulsory because these techniques reduce time and cost [41].

1) *Molecular markers development:* Molecular markers such as amplified fragment length polymorphism (AFLP) (Ayele et al., 1999), restriction fragment length polymorphism (RFLP) [42], ISSRs [43], and SSRs were used previously by many researchers to study teff genomics and genetics. These molecular markers are useful tools for studying variation analysis based on naturally occurring polymorphisms in DNA sequences to further enhance marker-assisted selection and breeding programs [44]. Molecular markers having high polymorphism are preferable; among these markers, SSR markers have been shown to be highly polymorphic within teff germplasm. Accordingly, the utilization of SSR rather than RAPD technology has improved the level of diversity in teff [45]. For instance, a genetic diversity study on 64 teff accessions collected from different parts of Ethiopia using 10 polymorphic SSR markers detected 314 total alleles with a mean value of polymorphic information content (PIC) of 0.87, indicating the existence of polymorphism for all loci [38].
2) *Development of genetic linkage maps:* Genetic maps are used to show the position of the molecular markers and QTLs relative to each other in terms of recombination frequency and are used to find genes responsible for traits of interest [22]. The efforts of mapping genetic linkage in teff began more than two decades and half ago and have progressed from complex sequence repeat (SSR) maps in 2011 to amplified fragment length polymorphism (AFLP) maps in 1999. For example, an RFLP linkage map using 116 RILs from the cross of 'Kaye Murri' with *E. pilosa* was developed in 2001. Accordingly, this inter-specific cross between Kaye Murri and *E. pilosa* produced far more polymorphisms; however, the main limitation is the level of polymorphism is still smaller than that of other grasses. Another study investigated that the RFLP map molecular genetic diversity demonstrated better genome coverage (88%) as compared with the previous AFLP map (81%) [42]. Additionally, a map from an interspecific cross (*E. tef* (DZ-01-2785) and *E. pilosa* (30-5)) was developed by utilizing a combination of different marker types, namely AFLP, ISSR, rice EST-SSR markers, and teff specific EST-SSR markers. The map was based on 124 F8 RILs and covered 78.8% of the genome.
3) Traits like grain yield, lodging resistance, seed weight, shoot biomass, and plant height are very important for the improvement of teff, and their QTL mapping was performed for the first time by [46]. The authors used 124 F8 recombinant inbred lines (RILs) from an inter-specific cross between *E. tef* and *E. pilosa* based on AFLP, ISSR, EST-SSR, and SSR markers. Accordingly, the percentage of phenotypic variance explained by the QTLs in this study ranged from 12.4% for a QTL associated with grain yield to 63.9% for a QTL associated with days to heading. Following this achievement, constructed the second QTL map for teff by using 94 F8 recombinant inbred lines (RILs) from the same mapping population. In this study, ninety-nine QTLs were identified, three times more than in the previous. The third QTL mapping in teff was conducted by using 151 F9 recombinant inbred lines and a PCR-based marker system. However, a marker system in which 83 QTLs were mapped on 30 linkage groups suffers from small marker density, and the QTLs are not validated and hence are of little use in initiating marker-assisted selection (MAS) in teff [47].
4) *Genetic regeneration and transformation*: The genetic transformation in teff started in the early 1990s, but the genetic transformation of teff was attempted without success. After a trial for a decade, a biolistic and agro-bacterium-mediated gene transfer in teff was reported with a successful genetic transformation and genetic regeneration [48]. Following this achievement, the first stable transformation of teff with GA inactivating gene PcGA2ox under the control of the CaMV 35S promoter using the Agrobacterium transformation was reported [49]. However, the challenges continue because there is no well-defined and reproducible transformation protocol developed for teff, and this needs further research. The teff research group established a reproducible transformation protocol at the University of Bern. The study conducted on the three teff genotypes revealed differential responses of callusing and regeneration efficiency. This study comprised Melko (drought tolerant), Gemechis (moderate), and POP12S2 (sensitive) and five levels of PEG (0, 0.5, 1, 1.5, and 2%) in which they screened for drought tolerance [50]. Accordingly, *in vitro* screening showed that regenerants of Melko (0.5%), Melko (1.5%), and Melko (1%) were drought-tolerant, while those of Pop12S2 (1.5%) were the most sensitive regenerants to moisture stress. The regenerants obtained from the Melko genotype under *in vitro* conditions may be used to develop drought-tolerant varieties in the future.

5) *High-Throughput Techniques:* While employing methods such as Targeting Induced Local Lesions IN Genome (TILLING) genome-specific primers are needed, which isolate homologous copies of each sub-genome, genome sequencing is particularly crucial [51, 52]. In the case of teff, the teff-TILLING project was initiated with financial support from the Syngenta Foundation for Sustainable Agriculture and the University of Bern and scientific collaboration with the University of Georgia, FAO/IAEA Programme, and Ethiopian Institute of Agricultural Research. The main goal of the project is to obtain semi-dwarf tetraploid teff lines that are resistant to lodging. So far, the project has generated over 4, 000 M2 mutagenized lines and utilized them in TILLING [53]. The generated mutants are used to develop desirable traits and further enhance the lacking genetic variation in the existing germplasms of teff. Some novel approaches that can enhance the teff breeding program include the improvement of agronomic practices, the creation of awareness for different stakeholders through training, field demonstration, and capacity building, and creating collaboration/linkage with national and international organizations/institutions [20].

2.4. Challenges of Teff Improvement Through Biotechnological Approach

The science of biotechnology is highly advancing and gaining popularity in crop improvement by solving breeding bottlenecks and fast-tracking conventional approaches. For instance, *in vitro* technology is applicable in germplasm conservation, distant hybridization (solving crossing barriers), and genetic transformation (using different vectors like Agrobacterium tumefaciens). However, cereal crops in general (monocots) and teff in particular benefited less from the science of biotechnology as compared to horticultural and other pulse crops (dicots) [54]. For example, many scholars developed biotechnological protocols to solve teff breeding challenges for important traits like lodging resistance, grain yield improvement, and seed size increment. Some achievements of teff improvement through a biotechnological approach were discussed under the molecular breeding approach.

The studies of plant cell and tissue culture on teff started in the 1990s'. The overall achievements and challenges of teff improvement through a biotechnological approach was recently reviewed by [54]. Previously, different authors reported the results of their work in which they used different explants and mediums. For instance, young seedlings root [55], leaf bases using MS medium at different concentrations. However, in those studies, young seedling root and leaf base segments, mature whole seeds, and immature spikelets demonstrated satisfactory improvement in *in vitro* culture responses with protocols involving MS or N6 basal induction medium supplemented with 1- 5 mg/l of auxins 2, 4-D or 3, 6-D or dicamba. In general, like other cereal crops, the invitro culture of teff is highly influenced by many factors, which include the type of explants used (roots, leaves, immature or mature embryos), growth stage, genotype, culture medium type and composition of culture medium, growth hormone and post culturing incubation, which needs further investigation and developing appropriate protocol [56].

2.5. Progress of Gene Editing Technology in Teff Improvement

Improvement of desirable traits through conventional breeding approaches is discouraging compared to modern breeding approaches like molecular breeding due to the following reasons, such as their labor intensiveness, time-consuming nature, less efficiency, and complexity (highly influenced by the environment). The challenges of the conventional plant breeding approach have been intervened through the development of techniques that enable gene knockout/in, epigenetic modifications, and the generation of heritable targeted mutations in specific genomic areas [57, 58]. Gene editing tools, such as Zink Finger Nuclease (ZFN), transcription activator-like effector nuclease (TALEN), and CRISPR/Cas9 (clustered, regularly interspaced short palindromic repeats), complemented the drawback of the conventional breeding approach [59]. Genome site specificity, cost-effectiveness, efficiency, and ease of execution are among the desirable properties of gene editing tools. From these three gene editing technologies (tools), CRISPR/Cas 9 fits these criteria and is preferable [60]. For instance, there are successful reports in many cereal crops, such as rice, wheat, maize, and barley, using CRISPR/Cas9 technology. recently reviewed the application of CRISPR to enhance genetic gain in orphan crops and identified the major challenges of this technology, like transformation efficiency and off-target mutation, which need further research. Particularly, *in vitro* regeneration and transformation are the major obstacles in orphan crops. However, in the sorghum crop, the possibility to regenerate a fertile plant from the engineered cell through tissue culture using Agrobacterium-mediated transformation is a recent breakthrough report. This technique breaks the barrier of genotype-dependent callus formation and shortens the time of the tissue culture cycle [61]. The gene editing tools have bottlenecks such as low plant regeneration efficiency even though they have many advantages, like improving important traits in crops like wheat and barley. For instance, the main challenge while using CRISPR/Cas9 is developing a transgene-free plant, which takes time until the T1 and T2 generations are obtained, and the efficiency of the procedure highly depends on the species of interest. But these challenges of CRISPR/Cas9 are tackled by using Growth Regulating Factor 4 (a plant-specific transcription factor), its factor GRT-Interacting Factor 1 (TaGIF1), and their chimeric proteins (Ta-GRF4-TaGIF1). This discovery significantly improved regeneration efficiency and reduced the time needed to accomplish the process in cereals like wheat, triticale, and rice, as well as increased the number of convertible genotypes [58]. The use of Wuschel2 (WUS2) and Babyboom (BBM) or together (BBM+WUS) makes possible transformation in grass species crops like maize, rice, teff, barley, rye, and sorghum, which indicates the possibility of using this technology in a teff improvement program for the improvement of challenging traits like lodging, small seed size, and grain yield [62]. However, the main challenge of teff improvement using gene-editing tools is the lack of fully annotated reference genomes in cultivated tef lines and the lack of efficient gene delivery plus regeneration methods. To date, the only reference genome available for a cultivated tef line is a draft genome of the 'Tsedey' (DZ-Cr-37) [63], and even this draft genome contains lots of challenges, such as fragmentation and missing sequence (Gebre et al., 2022). The next assignment to use and utilize the potential of recently developed gene editing tools in teff improvement should be searching reference genomes from related species or conducting extensive experiments in teff germplasms. The application of CRISPR/Cas9 in many cereals, pulses, and horticultural crops after its discovery has been increasing [19, 58].

2.6. Nutritional Composition and Health Benefits of Teff

"*Tef is a resilient crop from the Horn of Africa with significant importance in food and nutrition security, and currently gaining global popularity as health and performance food*" [14].

The grains of teff have high levels of proteins compared to the grains of wheat, maize, and pearl millet and greater than rye, brown rice, and sorghum [64, 65]. The nutritional profile of the teff grains, such as gluten-free and high content of dietary fiber, is among the most desirable and highly demanded at a global level, making teff the crop of choice as a source of healthy food because teff grains contain high and unique nutritional values that will meet the needs of health-conscious consumers [8]. Some reports indicated that 100 g of teff grains have 357 kcal, similar to that of wheat and rice [7]. In comparison to other cereals, teff grains are comparably rich in iron, calcium, and fiber, and an excellent source of proteins (essential amino acids), especially lysine: the amino acid that is most often deficient in grains [67]. For instance, teff grain, due to its low glycemic index, makes it suitable for people with Type 2 diabetes. Another study supported the absence of gluten in teff flour by the genome sequence initiative [63]. Additionally, the grains are also gluten-free, and this, in particular, attracts individuals who suffer from gluten intolerance or celiac disease [68]. Genomic loci associated with grain protein and mineral concentration were investigated by [30]. The results of the study revealed the influence of the environment, particularly water stress, which contributes effect on grain protein content and mineral concentration. The nutritional composition of teff as compared to other cereals is shown in Table 4.

Table 4. *Nutritional composition of teff as compared to the other major world cereals (100 g).*

Nutritional item	Teff	Finger millet	Rice	Maize	Wheat	Sorghum
Energy (cal.)	362.1	349.5	357	368.2	351.9	359.6
Moisture (%)	10.0	10.1	13	12.4	11.8	12.1
Protein (%)	11.0	7.2	7.3	8.3	11.2	7.1
Fat (%)	2.7	1.4	2.2	4.6	1.9	2.8
Carbohydrate (%)	71.0	73	64	71.2	70.6	74.1
Fiber (%)	3.0	5.0	0.8	2.2	3.0	2.3
Ash (%)	2.3	3.3	0.6	1.3	1.5	1.6
Ca (mg/100g)	165.2	386.0	6.0	6.0	49.0	30.0
P (mg/100 g)	366.0	220.0	140	276.0	276.0	282.0
Fe (mg/100 g)	18.9	85.1	0.8	4.2	7.5	7.8
Lysine	3.7	0.24	3.7	0.3	3.7	2.1
Isoleucine	4.1	0.39	4.1	0.7	4.5	3.7
Leucine	8.5	0.93	8.5	2.1	8.2	7.0
Valine	5.5	0.57	5.5	0.8	6.0	4.1
Phenylalnine	5.7	0.49	5.7	0.9	5.5	4.9
Tyrosine	3.8	-	3.8	0.7	5.2	2.3

Nutritional item	Teff	Finger millet	Rice	Maize	Wheat	Sorghum
Tryptophan	1.3	-	1.3	0.2	1.2	1.1
Threonine	4.3	0.39	3.7	0.41	2.7	0.5
Histidine	3.2	0.23	2.3	0.31	2.1	0.4
Arginine	5.2	0.38	8.5	0.50	3.5	0.6
Methionine	5.2	0.28	8.5	0.24	3.5	0.6
Cystine	2.5	-	1.8	-	2.4	0.3
Asparagines	6.4	-	9.0	-	5.1	-
Serine	4.1	0.48	5.0	0.57	5.0	0.8
Glum+gltamic	21.8	-	17.0	-	29.5	-
Proline	8.2	0.66	5.0	0.91	10.2	1.3
Glycine	3.1	0.33	4.5	0.40	4.0	0.5
Alanine	10.1	0.58	5.5	0.89	3.6	1.6

Sources: Compiled from [14, 65].

2.7. Existing Opportunities for Teff Breeding

"*Due to significant contributions of orphan crops in the economy of the developing world, scientific studies need to be promoted on these little researched but vital crops of small-holder farmers and consumers*" [18].

Teff has remained underutilized for centuries; however, it is getting global popularity among different stakeholders like consumers, researchers, and food processing companies due to its golden property of gluten-free and high dietary fiber content [66, 69]. For this reason, production of teff has been underway in different countries like India, China, Australia, Europe, and the United States as a healthy food and beverage production industry [8]. The demand for teff products is increasing both at the national and international levels [14]. There are factors that play a significant role for teff in demand. For instance, at a national level, the demand for teff is increasing due to: I) increasing population, which is estimated to be 100 to 130 million, II) improvement of people's livelihood and income, which enables the shift of diet from other cereals to teff. However, currently Ethiopian peoples are unable to afford teff due to inflation and Ethiopian birr devaluation. At international level, the demand of teff is highly increasing due to - III) the opening of peaceful reconstitution between the neighboring countries like Somaliland, Somalia and Eritrea (but recently stopped diplomatic relations with Eritrea while with of Soliland and Somalia are progressing well). IV) The global popularity for health benefits, particularly by the western countries and Ethiopian Diasporas. To ensure food security issues, which is a headache at global level, orphan crops are highly demanded due to their desirable traits. The four pillars of food security are - a) food availability, b) access to food c) food stability, and d) food utilization. The international scientific community, governments, private companies, and other stakeholders should work in collaboration to utilize the potential of orphan crops like teff and ensure food security. At continental level, Africa is highly risked by food security problem followed by Asia [18].

2.8. Challenges of Teff Breeding

The major challenges of teff breeding and production include the nature of the crop, like seed size (being very small/minute), the shattering problem (which causes major yield loss), difficulty in crossing (due to its floral biology), lack of mechanization in pre- and post-harvest technology, limited focus from national and international scientific communities, and lack of capacity building (limited trained professionals, infrastructures, and facilities), which are hindering its breeding progress and need research intervention [24]. Additionally, the method of sowing and seed rate affects teff productivity (hand broadcasting will leave seeds uncovered, leading to erosion by wind or rainfall), attack by birds, use of local unclean seeds, which leads to poor germination, lodging, which usually occurs after heading, the labor-intensive nature of the crop, and diseases like head smudge are also other constraints that challenge teff breeding [20]. Other challenges are related to the lack of satisfactory information on teff genetic resources, which means biogeography, taxonomy, evolution, conservation, and utilization. According to these authors, the above-mentioned teff breeding constraints/challenges are categorized into two major groups: 1) Technical constraints (these include low productivity, susceptibility to lodging, the labor-intensive nature of its husbandry practices, and biotic and abiotic factors). 2)

Socio-economic constraints (these include a lack of adequate attention given to its breeding activities, a weak seed and extension system, and unavailability of adequate agricultural inputs). Additionally, the progress of investment considering teff breeding and agronomic practices is scarce [40].

2.9. Why Teff Is Still Called Orphan Crop

The name 'orphan crops' refers to those without champions or crop experts [15]. There are also many other names given to these orphan crops [18]. To list some of them: underutilized (little researched) [70], neglected (little focus on science and development), traditional crops (used for centuries) [71], and future crops (high contribution to future food security) [72]. However, orphan crops are considered as 'miracle crops' for future farming and sustainability. These orphan crops are mainly cultivated in the least developed regions of the world, like Somalia, Sudan, Ethiopia, Eritrea, and Nigeria from Africa; Mongolia, China, Malaysia, Bhutan, and parts of India from Asia, South American countries; and some parts of Europe [73]. These orphan crops are very important, and their improvement can mitigate food security issues in the least developed countries, where food security issues are highly alarming [18]. This author addressed the need to invest in orphan crops due to their exclusion from the advanced research global agenda like the Green Revolution, less prioritized at the national level (for instance, teff vs. wheat cultivation in Ethiopian conditions). The author also discussed the major constraints related to orphan crops (inferior in productivity, poor unbalanced nutrition, toxic products, extreme environmental conditions), which need research intervention and merit related to orphan crops like suitability with socio-economy of the nation, and wider adaptability to climate change.

Although the scientific research in teff started in the 1950s' (as discussed earlier), it is still categorized as an orphan crop due to the following key reasons, such as localized importance (the teff crop is not prioritized in the global agenda due to its regional and local importance). At the domestic level, teff is a staple food and highly demanded and preferred by millions of Ethiopians. However, it has not been prioritized in the global agricultural agendas, like the Green Revolution, which typically favor stable crops with broader international markets [14], and limited genetic improvement (orphan crops like teff have benefited less from the genetic improvement initiative program compared to stable crops like rice, wheat, and maize, which have undergone intensive breeding operations). One factor contributing to teff's low production is the underutilization and under-exploration of its genetic diversity and potential, as well as challenges in cultivation (all activities of teff cultivation in Ethiopia are through traditional approaches; for instance, plowing and threshing are oxen-driven). Agronomic practices like sowing (difficulty of maintaining seed rate), harvesting, and threshing are tedious and time-consuming. Other difficulties discouraging teff-growing farmers are pests, drought, and lodging (the bending or breaking of stems), and less research (the scientific community of the world has not given teff the same level of attention as it has major crops like rice, wheat, and maize). This makes teff less amenable to genetic advancement and research. A lack of emphasis has also impeded breeding and agronomy developments, resulting in low yield productivity of teff (1.85 tons/ha) [18]. Therefore, the above-mentioned reasons should be intervened to exploit the potential of teff crop and make it a crop of choice at an international level. The following points were suggested by to improve orphan crops, particularly policy-related issues such as the implementation of the right type of strategy, investment in innovative agriculture, provision of inputs and credit, creation of a robust extension system, germplasm collection and utilization, developing crops that adapt to changing climates, and partnership with relevant stakeholders. The above-mentioned gaps, together with other factors, call for the necessity of intensive research and development on orphan crops like teff in order to unlock their potential. Teff has yet to complete its breeding progress and transition from the orphan crop category to the modern genomic era. However, if the aforementioned challenges are solved, it will enter into a modern breeding era very soon!

3. Conclusion and Way Forward

3.1. Conclusion

Ethiopia is the origin and center of diversity for teff (*Eragrostis tef* (Zucc.) Trotter) and many other oil and horticultural crops. Teff is one of the major staple cereal crops cultivated in Ethiopia, occupying more than three million hectares of land. While it ranks first in terms of area coverage, it ranks second and last in terms of production and productivity among the cereals under production in Ethiopia. Globally, only a few cereal crops are feeding the world population, and this leads to adverse food shortages and dietary imbalance. To intervene such problems, the diversification of food sources through utilizing underutilized crops like teff is getting attention.

Orphan crops are mostly cultivated in least developed countries where food security is a challenge, like Africa, Asia, and Latin America, while developed Western countries are looking for a lifestyle and healthier foods. Factors like population increment, pandemics, socio-economic disparities, competition for food and biofuel for existing land resources, and climate change are all worsening food security. To tackle these problems and ensure food security, the utilization of indigenous or "orphan" crops is important since these crops have the advantages that they are already well integrated into the socio-economics of the region. Farmers and consumers also prefer orphan crops like teff because they provide more stability under rapidly changing environmental conditions and demand.

Most Ethiopian farmers have been cultivating the teff crop for millennia due to its golden merits. Nowadays, it is getting more demand at the international level because of its gluten-free product. However, the productivity of teff is still very low as compared to other cereals like maize, sorghum, wheat, and rice. Scientific research on teff was initiated in the 1950s, and it has passed through five different phases to date. Many improved teff varieties (about 54) have been released to the farming community via conventional breeding approaches like mass/pure-line selection and hybridization; however, the molecular breeding approach of teff is at the infantile stage and needs further investigation in the future. The major challenges of teff breeding are categorized into two groups (technical and socio-economic constraints), which still need further research and remove teff from the category of orphan crops and make it an internationally prioritized crop.

3.2. Way Forward

In conclusion, conservation, characterization, utilization, and germplasm enhancement of teff are very important because the chance of introducing teff germplasm and related resources from abroad is rare. Additionally, complementary breeding approaches like the participatory breeding approach, conventional, and molecular should be encouraged to improve the productivity of teff and tackle its production constraints. The recently developed gene editing tools, like CRISPR technology, are promising to enhance breeding in other cereal crops like rice, wheat, and maize. Implementing this technology in teff and other orphan crops will solve the current food security problems. Therefore, researchers (both national and international scholars of the discipline), governments, companies, private sectors, and other stakeholders should invest in orphan crops like teff to utilize their potential and secure food availability for all nations.

Abbreviations

AOCC	African Orphan Crops Consortium
CSA	Central Statistical Agency
FAO	Food and Agricultural Organization
NRC	National Research Council
QTL	Quantitative Trait Loci
RIL	Recombinant Inbred Line

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Author Contributions

Morketa Gudeta Waktola: Conceptualization, Investigation, Methodology, writing original draft, review and editing

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Data Availability Statement

The original contributions presented in the study are included in the article; further inquiries can be directed the corresponding author.

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Conflicts of Interest

The authors declare no conflicts of interest.

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