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REVIEW

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Value of teff (*Eragrostis tef*) genetic resources to support breeding for conventional and smallholder farming: a review

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Abstract

Crop germplasm collections are a key asset to support the resilience and productivity of cropping systems worldwide. In their diversity lays an oftentimes untapped reservoir of alleles that may enable breeding strategies targeting local adaptation, resulting in enhanced performance and higher varietal uptake. In the past five decades, the national genebank of Ethiopia actively collected and conserved thousands of teff (*Eragrostis tef*) accessions, a staple crop throughout the Horn of Africa at the basis of countless cultural uses and with high market relevance. This review article emphasizes the breeding significance of teff genetic resources, highlighting current challenges in teff farming and improvement that could be addressed further valorising germplasm collections. We collect data generated on the largest teff ex situ collections in the world to discuss opportunities to improve teff tolerance to stress and lodging, as well as to increase its productivity across its cropping area. In doing so, we highlight and critically revise current and past literature tapping in teff diversity to support teff improvement. This review starts providing a summary of teff characteristics, detailing the status and challenges of teff cultivation and breeding. It then follows describing the diversity existing in teff diversity collections and its relevance for teff improvement. The review concludes describing the molecular studies undertook on teff in the past two decades, highlighting the perspectives of molecular breeding for teff. The body of knowledge available on teff shows that there is large potential for improvement of this crop to target smallholder farming systems as well as international markets, and that improvement may start from the large diversity available in teff collections.

Keywords: *Eragrostis tef*, Teff, Ex situ, Agrobiodiversity, Breeding, Smallholder agriculture, Neglected and underutilized crops

Introduction

Teff (*Eragrostis tef* Zucc., $2n = 4x = 40$) is a C_4 cereal crop that has been cultivated in the Horn of Africa since millennia (Harlan 1969). In Ethiopia, teff is a staple crop for about 70 million people (Assefa et al. 2011), as well as a source of feed (Yami 2013) and a cash crop generating incomes for about $0.5 B per year in the local smallholder farming system (Bayissa 2018). Teff flour is rich in proteins and minerals (Bultosa 2007), making it prized as a gluten-free *superfood* in western countries (Tietel et al. 2020; Gebru et al. 2020). As a consequence, teff is increasingly under the lens of local and international research to support its cultivation and commercialization (Chanyalew et al. 2019).

In Ethiopia, teff stands first in the total area cultivated and second to maize for total grain production and number of households producing it, but last in term of yield per area unit (Central Statistical Agency 2018). Its

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current average productivity is well below its genetic potential: improved cropping technologies in non-lodging conditions can result in yields exceeding 4.5 t ha^{-1} (Tefera and Ketema 2001), more than double the national average (Central Statistical Agency 2018). However, teff yield potential can be fully achieved only when applying appropriate sowing and plant curation (Ben-Zeev et al. 2020; Mihretie et al. 2021; Bogale et al. 2013), management of soil fertility (Wato 2019), and appropriate agronomic practices (Gezahegn et al. 2019; Berhe et al. 2013) including weed management (Rezene and Zerhun 2000) and pest management (Gemechu Degete 2021; Gyan et al. 2020).

Notwithstanding a large body of knowledge has been developed around the best practices for teff management, much progress can still be done in regards of its genetic improvement. Teff can be well considered a neglected and underutilized species (NUS) (Bachewe et al. 2019; Tadele 2018), a crop for which much potential exists still undisclosed by modern breeding approaches. It did not benefit of the leap forward of the green revolution that revolutionised the yields of other cereals, including the closely related rice and wheat. This depends on many factors, including the fact that only recently teff has been brought under the focus of the international scientific community. Nowadays, a complete teff genome produced using third generation genomics is available (VanBuren et al. 2020), and complements a draft genome published a few years ago (Cannarozzi et al. 2014).

As is the case of other NUSs, teff germplasm shows high variation for several useful traits that are seldom present in improved lines derived by formal breeding efforts (Jifar et al. 2018; Woldeyohannes et al. 2020). The diversity in teff germplasm, including wild relatives, landraces, and farmer varieties, is a reservoir of allelic diversity that once properly characterized may boost teff breeding (Girma et al. 2014; Cannarozzi et al. 2018) (Fig. 1). Teff landraces diversity is connected with the climatic variation existing across its growing area and to the socio-cultural process linked to its cultivation and trade (Woldeyohannes et al. 2020). Being mainly cultivated in a smallholder farming system with negligible use of agronomic inputs, teff germplasm has evolved at the interface of human and natural selection, accumulating variation useful to make it adapted to a range of abiotic and biotic stresses (Woldeyohannes et al. 2020), and including resistance to various pests (Chanyalew et al. 2019).

This review emphasizes the breeding significance of teff genetic resources as a possible approach to address known challenges of teff farming. The first part of the review discusses the value of teff cultivation, its main constraints, and the status of conservation of teff genetic resources. The second part of the review provides a detailed description of the potential of teff genetic

Fig. 1 An experimental field with 3850 teff landraces sourced from the EBI collection, at grain filling stage (West Gojam, Amhara, Ethiopia, 11° 16′ 32″ North, 37° 29′ 30″ East) (Woldeyohannes et al. 2020)

resources to improve key target traits. The concluding part of the review details molecular studies conducted in teff to support advanced breeding methods. We conclude discussing how teff diversity may be accessed with modern research approaches to maximize its agronomic performance, local adaptation, and farmers' appreciation.

Status of teff cultivation and agrobiodiversity conservation

Appeal of teff cultivation and consumption

Teff is currently cultivated in Ethiopia by about 6.7 million rural households over 3 M ha, more than double the area that was allocated to its production in the 1990s (Central Statistical Agency 2018). The appeal of teff cultivation in the Ethiopian highlands has several reasons. Due to its capacity for local adaptation, teff is considered a low-risk crop by local farmers (Yihun et al. 2011). Early maturing cultivars are commonly used in areas with a short growing period, often as a replacement crop at times of failures of higher yielding long-season crops (e.g. maize). Early maturing teff cultivars have also a practical functionality for doubling with other cropping systems in high rainfall areas allowing for cultivation of pulses and oil crops (Ketema 1997). However, farmers may choose teff also for economic and nutritional considerations. In formal and informal markets, teff grain and straw fetch higher prices as compared to those of other cereal crops. Its flour is used for food preparations including *injera* (traditional circular, thin, fermented pancake), *kitta* (unleavened bread), *porridge*, *muk* (a kind of soup) and *talla* (local beer) (Ebba 1969). Teff flour is prized as it is highly nutritious and rich in minerals, fat and proteins, and micronutrients (Bultosa 2007; Gebru et al. 2020). Its straw, when used for feed, is also desirable due to low lignin content and high quality for crude protein content, in vitro dry matter digestibility, and energy value (Yami 2013).

The manifold advantages of teff cultivation and consumption make it a valuable resources to contrast malnutrition (Abewa et al. 2019) as well as a crop with high potential for global health food consumers (Lee 2018). The demand for gluten free foods is growing and expanding as more people are diagnosed with celiac disease and other types of gluten sensitivity (Bascuñán et al. 2020), making teff-derived bakery products ever more desirable in the western world and even a candidate for malting and brewing (Cela et al. 2020; Gebremariam et al. 2014).

Challenges of teff farming

Teff mean yield across Ethiopia, at 1.76 t ha^{-1}, is much lower than that of other cereals cultivated in the same area (e.g. maize 3.9 t ha^{-1}, wheat 2.7 t ha^{-1}, sorghum 2.7 t ha^{-1} and barley 2.1 t ha^{-1}) (Central Statistical Agency 2018). Teff low productivity is due to several production challenges that exist unchanged since thousands of years, some of which exacerbated by climate change (Table 1).

Lodging is arguably the major bottleneck for teff farming (van Delden et al. 2010; Assefa et al. 2015; Wrigley et al. 2006). It is ultimately caused by the insufficient resistance of sclerenchyma in the culms, leading to failure to support grain bearing panicles when they become too heavy. Lodging is exacerbated by supplements of fertilizer, damage to the root system, heavy rates of seedling, and lack of nutrients (Rajkumara 2008), and affects yield quality and quantity by interfering with water and nutrient transport as well as with light interception (Ketema 1997). Soil features, including water availability, are the second most prominent limitation to teff cultivation. Low moisture deficit can indeed negatively impact teff growth, particularly at flowering and grain filling stages (Araya et al. 2011). In the western part of Ethiopia and in the highlands, soil acidity severely affects teff productivity, lowering teff response to fertilizer application (Abate et al. 2017). Biotic factors may also challenge teff cultivation, although they are less studied. Teff diseases include rust (*Uromyces eragrostidis* Tracy), head smudge (*Helminthosporium miyakei* Nisikado), damping-off (*Drechslera* spp.) and leaf spot (*Helmithosporium* spp.) (Badebo 2013; Gemechu 2018; Gemechu Degete 2021). Insect pests can also impact teff production, especially teff grasshoppers (*Aiolopus longicornis, Aiolopus thalassinus*), teff shoot flies (*Elachiptera simplicipes, Melanochaeta vulgaris, Oscinella nartschukiana*), teff red worm (*Mentaxya ignicollis*), wollo bush cricket (*Decticoides brevipennis Ragge*), and termites (*Macrotermus subhyalinus* and *Odontotermus* spp.) (Damte 2013).

The climate crisis may exacerbate current teff cultivation constrains, exposing the agroecosystems in the Horn of Africa to abiotic stresses potentially altering their productivity and function. In Ethiopia, farmers already

Table 1 Extent of estimated yield losses by cause in teff growing areas in Ethiopia

Stress	Estimated yield loss (%)	References
Drought	26 to 58	Ferede et al. (2018)
Soil acidity	46	Abewa et al. (2013)
Soil salinity	32 to 91	Asfaw et al. (2011)
Lodging	11 to 27	Ketema (1997)
Weed	21	Gebrehiwot et al. (2020)
Shoot fly	13 to 24	Damte (2013)
Wello Bush Cricket	15 to 37	Damte (2013)
Teff Red Worm	24 to 30	Damte (2013)
Teff Rust	10 to 41	Dawit and Andnew (2005)

favour drought tolerant crops and varieties to adapt to climate change, a pattern expected to consolidate (Marie et al. 2020). Climate change may also have an indirect effect through changes in the number, distribution patterns and virulence of pests and diseases (Black et al. 2011). Recent studies shown that teff cultivation suitability may diminish by 2070, urging long-term planning of breeding decisions (Woldeyohannes et al. 2020, 2021). In this scenario, the lack of improved varieties for specific environments (Assefa et al. 2015) calls for a more coherent characterization and utilization of teff genetic resources.

Ex situ and in situ conservation of teff germplasm

Ethiopia is the domestication center for *E. teff* (Harlan 1928) and a systematic collection, evaluation, and utilization of teff germplasm began in Ethiopia in the late 1950s. For the past five decades, the Ethiopian Biodiversity Institute (EBI) has collected and conserved a significant number of teff accessions, much exceeding those available ex situ in other gene banks (Table 2).

Although the large number of teff accessions currently conserved at EBI, the exploitability of this resource may be further improved. Inside this gene bank, that operates at the highest international quality standards (Thomas et al. 2019), several accessions lack part of the passport information (Girma et al. 2014). A recent study reported that out of the 3850 teff accessions representing the active collection from the EBI, amounting to about 60% of the full collection, complete passport information was available for 1754 accessions (Woldeyohannes et al. 2020). Teff ex situ accessions can be in some cases duplicates, as the genetic redundancy of accessions between and within institutions is not fully known. Furthermore, most accessions lack information related to traditional name and farmers knowledge on the specific landrace, a feature that may be considered useful in designing further sampling campaigns to assess ethnographic significance of the accessions (Roncoli 2006). Wild species are seldom included in sampling campaigns and are not featured in the EBI collection: out of the 350 species in the genus *Eragrostis*, 14 are endemic to Ethiopia (Costanza et al. 1979) and may have high genetic diversity relevant for teff conservation and improvement (Girma et al. 2018).

Expanding teff collections is still a critical endeavor. In situ, the quick spreading of improved varieties of teff (e.g. *Quncho*) may permanently replace teff landraces in several agroecologies (Assefa et al. 2011). Moreover, in the absence of teff breeding materials with enhanced tolerance to biotic stresses such as soil acidity, the switch towards adoption of acidophilic crops may further accelerate the loss of teff genetic resources in regions where these stresses are prominent (Abate et al. 2017). All these developments call

Table 2 Summary of 7235 teff accessions currently conserved ex situ in germplasm banks worldwide, with an estimate of passport data completeness

Country	Holding Institute/ Code	Institute homepage	Number of accessions	Passport information (%)	
				Collection site	GPS
Ethiopia	EBI	https://www.ebi.gov.et/	6407	68	48
Israel	ISR002	NA	376	NA	NA
United states of America	USA022	https://www.ars-grin.gov/	373	91.4	3
Germany	DEU146	https://www.ipkgatersleben.de/	32	3	12.5
Australia	AUS165	NA	20	NA	NA
Australia	AUS167	https://www.pir.sa.gov.au/	12	8.3	NA
Ethiopia	ETH013	https://www.ilri.cgiar.org/	3	NA	NA
Hungary	HUN003	https://www.rcat.hu/	3	NA	NA
Kenya	KEN212	https://www.genetic.kalro.org/	3	66.6	33
Austria	AUT001	https://www.genbank.at/	2	50	NA
United Kingdom	GBR016	https://www.igergru.ibers.aber.ac.uk/	2	NA	NA
Bulgaria	BGR001	https://www.genebank.hit.bg/	1	NA	NA
Czech Republic	CZE122	https://www.vurv.cz/	1	NA	NA

An estimated proportion of accessions having passport data available in regards of collection site and GPS coordinates is given when available (Source: obtained from (https://www.ebi.gov.et/ and https://www.genesyspgr.org/). All data is up to date to 2021 except for EBI data (2016)

NA: Not available; EBI: Ethiopia Biodiversity Institute, Ethiopia; ETH013: International Livestock Research Institute, Ethiopia; ISR002: Israel Gene Bank for Agricultural Crops, Agricultural Research Organization, Volcani Center, Israel; USA022: Western Regional Plant introduction Station, USDA-ARS, Washington State University, USA; DEU146: Leibniz Institute of Plant Genetics and Crop Plant research, Germany; AUS165: Australian Grains Genebank, Department of Economic Development Jobs Transport and Resources, Australia; AUS167: Australian Pastures Genebank, Australia; HUN003: Institute for Agrobotany, Hungary; KEN212: Genetic Resources Research Institute, Kenya; AUT001: AGES Linz-Austrian Agency for Health and food Safety, Austria; GBR016: Genetic Resources Unit, Institute of Biological, Environmental and Rural Sciences, Aberystwyth University, UK; BGR001: Institute for Plant Genetic Resources K. Malkov, Bulgaria; CZE122: Gene Bank, Czech Republic for urgent and constant updating and a further expansion of teff germplasm collections. Today, most of the EBI teff collection derives from sampling associated with the main roads of Ethiopia. A geographic information system (GIS) analysis looking at the intersection of EBI teff georeferenced accessions and the road network in Ethiopia shows that 61.7% of the accessions with GPS coordinates were collected within 500 m and 87.7% within 2000 m from the nearest road, leaving behind potentially relevant teff adaptation zones in remote areas (Fig. 2). This is a quite common feature of ex situ collections, and for good reasons of cost-effectiveness of sampling campaigns (Kasso and Balakrishnan 2013). However, future sampling campaign may focus on more remote areas, targeting the extremes of teff distribution (e.g. exceptionally low or high-altitude ranges) to harness additional adaptive teff variation of breeding relevance.

Teff breeding and diversity in ex situ collections

Teff research and breeding started in 1956 at the Jimma Agricultural and Technical High School, now Jimma Junior College of Agriculture. In 1960, it was transferred to the Central Agricultural Experiment Station, now the Debre Zeit Agricultural Research Centre. Since then, 49 improved varieties have been released (Ministry of Agriculture and Livestock Resources 2019). Of these, 25 were derived from farmer cultivars through mass selection, while the rest were obtained via conventional hybridization programs (Table 3). Throughout the teff breeding program, grain yield increased at an average of 0.8% to 0.9% per year (Teklu and Tefera 2005; Dargo et al. 2016). Varieties developed with hybridization yield 9% greater than those obtained through direct selection from germplasm, indicating that grain yield can be enhanced by active breeding (Assefa et al. 2013).

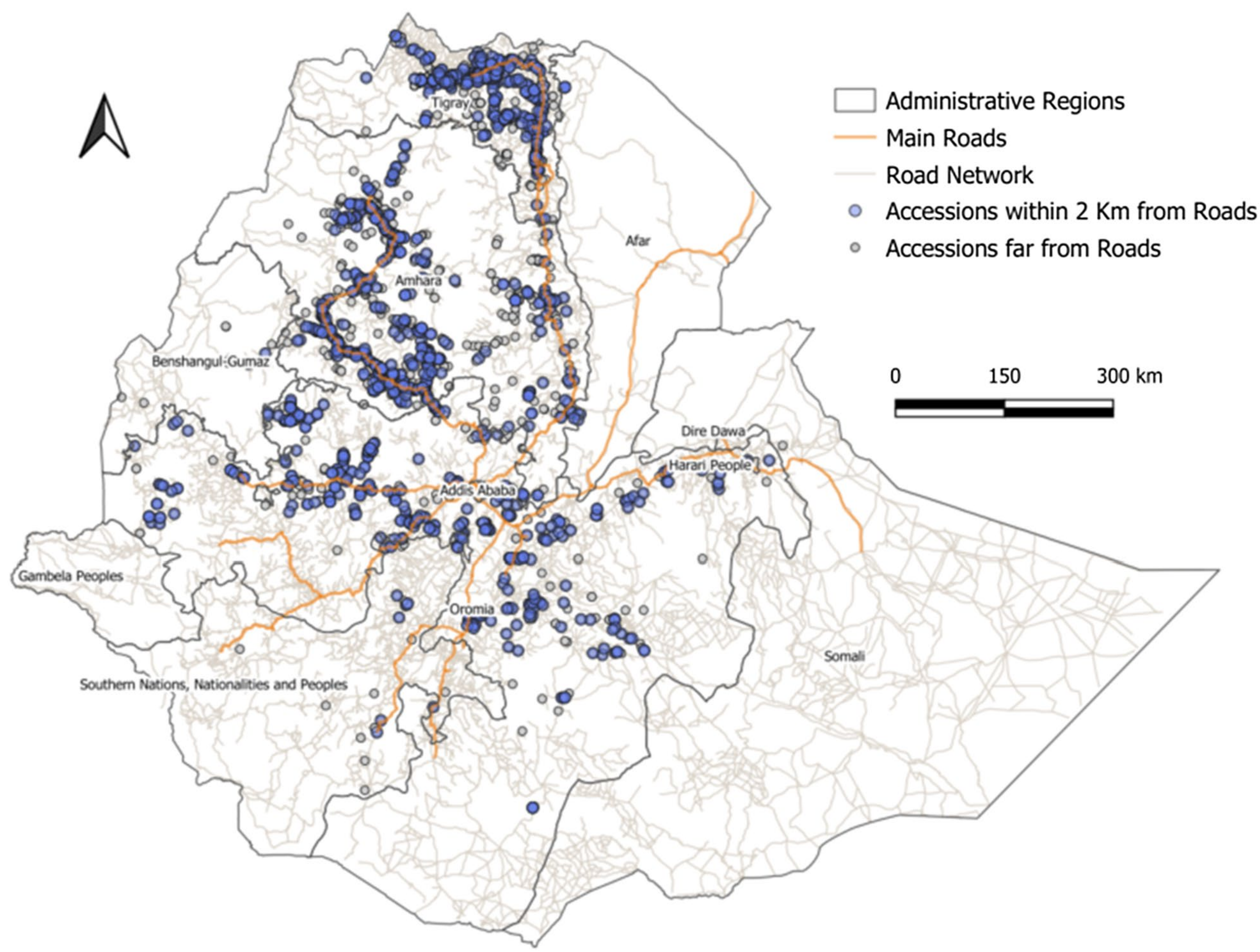

Fig. 2 A map showing sampling points of a selection of 1754 teff accessions in the EBI collection overlaid to the Ethiopian road network. The EBI ex situ teff collection is the largest in the world, and a remarkable display of Ethiopian teff agrobiodiversity. Future national and international sampling efforts may focus on secluded areas far from the road network to capture additional teff diversity. Data from (Woldeyohannes et al. 2020)

Table 3 List of modern teff varieties developed and released in Ethiopia by national and regional Agricultural Research Center until 2019 (Ministry of Agriculture and Livestock Resources 2019)

Variety name	Pedigree	Seed color	Days to maturity	Grain yield (t/ha)		Method	Center	Recommended production areas	Release year
				Research field	Farmer field				
Asgori	DZ-01-99	Brown	80–130	2.2–2.8	1.8–2.2	Selection	DZARC	High potential	1970
Enatite	DZ-01-354	Pale white	85–100	2.4–3.2	2–2.4	Selection	DZARC	High potential	1970
Magna	DZ-01-196	Very white	80–113	1.8–2.4	1.6–2	Selection	DZARC	High potential	1978
Wellen-komi	DZ-01-787	Pale white	90–130	2.4–3	2–2.4	Selection	DZARC	High potential	1978
Menage-sha	DZ-Cr-44	White	95–140	1.8–2.4	1.8–2.2	Hybridization	DZARC	High potential	1982
Melko	DZ-Cr-82	White	112–120	1.8–2.4	1.6–2	Hybridization	DZARC	High potential	1982
Tsedey	DZ-Cr-37	White	82–90	1.8–2.5	1.4–2.2	Hybridization	DZARC	Moisture deficit	1984
Gibe	DZ-Cr-255	White	114–126	2–2.6	1.6–2.2	Hybridization	DZARC	High potential	1993
Ziquala	DZ-Cr-358	White	76–138	2.4–3.4	2–2.7	Hybridization	DZARC	High potential	1995
Dukem	DZ-01-974	White	75–137	2.4–3.4	2–2.7	Selection	DZARC	High potential	1995
Holetta Key	DZ-01-2053	Brown	84–112	1.7–2.4	1.5–2.2	Selection	HARC	High potential	1998
Ambo Toke	DZ-01-1278	White	75–112	1.7–2.4	1.5–2.2	Selection	HARC	High potential	1999
Key Tena	DZ-01-1681	Brown	84–93	1.7–2.4	1.6–2.2	Selection	DZARC	Moisture deficit	2002
Gerado	DZ-01-1281	White	73–95	1.7–2.4	1.6–2.2	Selection	DZARC	Moisture deficit	2002
Koye	DZ-01-1285	White	104–118	1.7–2.4	1.6–2.2	Selection	DZARC	High potential	2002
Gola	DZ-01-2054	Pale white	82–90	1.4–1.9	1.2–1.6	Selection	SARC	Moisture deficit	2003
Ajora	PGRC/E205396	Pale white	89–96	1.4–2	1.6–1.8	Selection	ARARC	Moisture deficit	2004
Dega Tef	DZ-01-2675	Pale white	112–123	1.5–2.4	1.4–2.2	Selection	DZARC	Highland	2005
Dima	DZ-01-2423	Brown	92–106	1.7–2.3	1.6–2.1	Selection	AARC	High potential	2005
Genete	DZ-01-146	Pale white	75–87	1.4–2	1.2–1.6	Selection	SARC	High potential	2005
Gimbichu	DZ-01-899	Pale white	118–137	1.5–2.2	1.6–2	Selection	DZARC	Highland	2005
Yilmana	DZ-01-1868	Pale white	98–110	1.8–2.4	1.7–2	Selection	AARC	High potential	2005
Zobel	DZ-01-1821	White	72–87	1.4–2	1.3–1.8	Selection	SARC	Moisture deficit	2005
Quncho	DZ-Cr-387RIL355	Very white	86–151	2–3.2	1.8–2.6	Hybridization	DZARC	High potential	2006
Amarach	HO-Cr-136	Pale white	63–87	1.8–2.5	1.4–2.2	Hybridization	DZARC	Moisture deficit	2006
Guduru	DZ-01-1880	White	95–120	1.8–2.2	1.6–2	Selection	BARC	High potential	2006
Gemechis	DZ-Cr-387/RIL127	Very white	72–95	1.5–2	1.6–1.8	Hybridization	MARC	Moisture deficit	2007
Mechare	Acc. 205953	Pale white	78–85	1.5–2.1	1.4–1.8	Selection	SARC	Moisture deficit	2007
Etsub	DZ-01-3186	White	95–105	1.9–2.4	1.9–2.4	Selection	AARC	High potential	2008
Kena	23-Tafi-Adi-72	White	98–124	1.8–2.4	1.7–2.2	Selection	BARC	High potential	2008
Laketch	RIL273	Very white	87–92	1.7–2.2	1.8–2	Hybridization	SARC	Moisture deficit	2009
Simada	DZ-Cr-385/ RIL 295	White	75–87	22–2.8	1.6–2.4	Hybridization	DZARC	Moisture deficit	2009
Boset	DZ-Cr-409/RIL50d	Very white	75–86	1.9–2.6	1.8–2.4	Hybridization	DZARC	Moisture deficit	2012
Kora	DZ-Cr-438/RIL133B	White	113	2.5–3.2	2–2.8	Hybridization	DZARC	High potential	2014
Werekiyu	Acc.214746	White	90–94	2.2	1.6	Selection	SARC	Moisture deficit	2014
Abola	Quncho*Key muri	White	110–118	2.1–2.8	1.5–1.7	Hybridization	AARC	High potential	2015
Dagem	DZ-Cr-438 /RIL91A	White	114	2.5	NA	Hybridization	DZARC	High potential	2016
Tesfa	DZ-Cr-457(RIL.181)	Very white	103	2.5	2–2.4	Hybridization	DZARC	High potential	2017
Hiber-1	DZ-01-974*P1222988	Very white	112–124	2.2–2.7	NA	Hybridization	AARC	High potential	2017
Areka-1	Dz-01-974*DZ-01-2788	White	112–119	2–2.6	NA	Hybridization	ARARC	High potential	2017
Felagot	DZ-Cr-442 (RIL.77C)	Brown	126	2.5	NA	Hybridization	DZARC	High potential	2017
Niguse	DZ-Cr-429(RIL.125)	Very white	112–116	2–2.6	NA	Hybridization	DZARC	High potential	2017
Abay	Acc ≠ 225931	White	95–132	25–35	18–22	Selection	AARC	High potential	2018
DURSI	Acc ≠ 236952	Cream white	132	20–24	18–22	Selection	BARC	High potential	2018

Table 3 (continued)

Variety name	Pedigree	Seed color	Days to maturity	Grain yield (t/ha)		Method	Center	Recommended production areas	Release year
				Research field	Farmer field				
Washera	353*Key muri (RIL29)	Very white	108–125	23–32	19.8–24.7	Hybridization	AARC	High potential	2019
Jitu	DZ-01-256	Pale white	120	21.3–25.3	19.6–23	Hybridization	BARC	High potential	2019
Bora	DZ-Cr-387(Quncho) × 3774-13(RIL No. 12B)	Very white	90	2.7	NA	Hybridization	DZARC	Moisture Deficit	2019
Mena	DZ-01-354xDZ-CR-37-131	Yellowish white	80–86	24–30	20–25	Hybridization	SARC	Moisture deficit	2019
Ebba	Key muri × 3773-13 (RIL No. 18)	Very white	98–110	20–26	19–23	Hybridization	DZARC	High potential	2019

Acc: Accession; AARC: Adet Agricultural Research Center; ARARC: Areka Agricultural Research Center; BARC: Bako Agricultural Research Center; DZ-Cr: Debre Zeit Cross; DZARC: DebreZeit Agricultural Research Center; HARC: Holleta Agricultural Research Center; MARC: Melkassa Agricultural Research Center; SARC: Sirinka Agricultural Research Center

In any crop, the success of varietal improvement is function of the combination and interaction of several components of agronomic performance. Literature reports show that most of teff traits are interrelated with one another and often changes in one trait are likely to influence others, so that the net gain obtained by selecting for a phenotype may be counter balanced or even negated by a simultaneous change in the others (Table 4).

Due to the enormous diversity in teff genetic resources available to breeders, and due to the relatively early stage of its improvement, several reports have focused on the diversity of teff collections. We have discussed how much of teff cultivation in the Horn of Africa depends on landraces and traditional varieties that farmers select and propagate since centuries. As a result, landraces acquired traits for local adaptation that could be very relevant for breeding. The diversity included in these landraces is very large for agronomic traits, adaptation traits, and farmer preference (Woldeyohannes et al. 2020, 2021). Below, we discuss extant variation reported in landrace collections and breeding materials for key improvement traits.

Lodging

Lodging is arguably the most important bottleneck for teff improvement. This issue becomes more prominent with increased yield, panicle size, and biomass (Tefera et al. 2003; Muluken et al. 2020) and is exacerbated by fertilization in high input areas (Assefa et al. 2015; van Delden et al. 2010; Chanyalew et al. 2019). Lodging in teff is mainly due to stem failure, as shown by the fact that root lodging is seldom present (Muluken et al. 2020) and that varieties with compact panicles and reduced height have increased lodging resistance (Blösch et al. 2020). Reduced plant stature is therefore a main breeding target in teff. Teff genetic resources bear large variation for stem biomechanical traits that can contribute to lodging resistance (Muluken et al. 2020). Culm internode diameter may vary substantially (from 1.2 to 5 mm) (Ebba 1975), and thicker stems may also contribute to support higher panicle weight. Lodging resistant genotypes were produced though mutagenesis, successfully reducing plant height (Cannarozzi et al. 2018) and achieving high yield potential (Jifar et al. 2017).

Panicle traits

Teff yield is positively associated with panicle size, floret abundance, and shoot biomass (Chanyalew et al. 2009; Jifar et al. 2015; Ferede 2013). Longer panicles are preferred by farmers in agroecologies that allow longer vegetative growth, as they may result in higher yields (Tefera et al. 1990). Indeed, breeders may predict yield potential from panicle features (Adnew et al. 2005). Still, the rate of change of panicle traits in breeding is not sufficient per se in enhancing overall grain yield (Teklu and Tefera 2005). Large variation exist in teff collections for panicle related traits, including spikelet length (3 to 15 mm), spikelet width (1 to 3 mm), lemmas length (2 to 3 mm), lemmas width (1.3 to 2.03 mm) (Ebba, 1975) and number of grains per panicle (1520 to 6652) (Tefera et al. 1990). The EBI teff collection features accessions exhibiting very different panicle types, from very compact to extremely loose (Woldeyohannes et al. 2020) (Fig. 3). Compact types have a high spikelet number per panicle and are frequently cultivated under more favourable conditions (Woldeyohannes et al. 2020), however loose types can also be high yielding (Tefera et al. 1990).

Plant and root architecture

At present, plant stature of teff is positively correlated with achieved grain yield (Tadele et al. 2013; Chanyalew et al. 2009; Tefera et al. 2003; Muluken et al. 2020). This

Table 4 Trait associations reported in *Eragrostis* literature

Genetic materials	Trait	Associated variables	Association	References
163 RILs	Grain yield	DH, DM, PH, PL, SB, CL, NCI, LFCL, SCL, FCD, SCD, PW, LI	Positive	Tefera et al. (2003)
60 genotypes	Grain yield	DH, DM, CD, PL, NPB, FPS, SPP	Positive	Assefa et al. (2002)
10 improved varieties	Grain yield	BY, SPP, PY	Positive	Teklu and Tefera (2005)
10 improved varieties	Grain yield	KPS	Negative	Teklu and Tefera (2005)
15 landraces	Grain yield	HGW, PH, PL/SB, NIC, HI	Positive	Tadele et al. (2013)
36 brown-seeded genotypes	Grain yield	DH, GFP, DM, PL, SB, HI	Positive	Jifar et al. (2015)
6 teff genotypes	Grain yield	Excised leaf water loss	Negative	Teferra et al. (2000)
24 semi-dwarf teff lines	Grain yield	DM, PH, CL, PL, PDL, SCL, SCD	Positive	Jifar et al. (2017)
196 RILs	Plant height	DH, PL, SB	Positive	Chanyalew et al. (2009)
15 landraces	Plant height	SB, HSW, HI	Positive	Tadele et al. (2013)
320 teff genotypes	Plant height	LI, PR, BS	Positive	Muluken et al. (2020)
320 teff genotypes	Tiller number	LI, BS	Negative	(Muluken et al. 2020)
24 semi-dwarf teff lines	Fertile tiller	DH, DM	Negative	Jifar et al. (2017)
24 semi-dwarf teff lines	Fertile tiller	PH, CL, PL, PDL, SCD	Positive	Jifar et al. (2017)
36 brown-seeded genotypes	Culm length	DH, DM, GFP, PL, GY	Negative	Jifar et al. (2015)
3850 landraces	Panicle length	Precipitation, DH, DM	Positive	Woldeyohannes et al. (2020)
163 RILs	Peduncle length	CL, PL, PH, FCL, SCL, CDF, CDS	Positive	Tefera et al. (2003)
24 semi-dwarf teff lines	Lodging index	DH, DM, CL, PDL	Positive	Jifar et al. (2017)
24 semi-dwarf teff lines	Spikelet per panicle	PH, CL, PL, PDL, SCL, SCD	Positive	Jifar et al. (2017)
24 semi-dwarf teff lines	Spikelet per panicle	DH	Negative	Jifar et al. (2017)
24 semi-dwarf teff lines	Thousand kernel weight	SCD	Positive	Jifar et al. (2017)
24 semi-dwarf teff lines	Thousand kernel weight	DH, DM	Negative	Jifar et al. (2017)
3850 landraces	Grain filling period	Temperature	Negative	Woldeyohannes et al. (2020)
60 genotypes	Harvest index	DM, GFP, SPP, GYPP	Negative	Assefa et al. (2002)
3850 landraces	Altitude	Temperature	Negative	Woldeyohannes et al. (2020)
3850 landraces	Soil pH	Altitude, precipitation	Negative	Woldeyohannes et al. (2020)
3850 landraces	Brown seed	Altitude, soil acidity	Positive	Woldeyohannes et al. (2020)
3 species of *Eragrostis*	Leaf tensile strength	Drought tolerance	Positive	Balsamo et al. (2006)
6 teff genotypes	Drought susceptibility index	ELWL, RGR	Positive	Teferra et al. (2000)
45 cultivars	Root depth	SW, RW, PH, CD, CT, RT, RSR, RLD, TN	Positive	Ayele et al. (2001)
45 cultivars	Root length density	SW, RW, RN, RSR, TN	Positive	Ayele et al. (2001)
45 cultivars	Root length density	Longer duration of teff survival	Positive	Ayele et al. (2001)
16 genotypes	Osmotic adjustment	LTR, RGR	Positive	Degu et al. (2008)
16 genotypes	Maximum root length	LTR, RGR	Positive	Degu et al. (2008)
12 cultivars	Canopy temperatures	ELWL	Negative	Takele (2001)
12 cultivars	Canopy temperatures	Grain yield	Negative	Takele (2001)
12 cultivars	ELWL	Grain yields under moisture deficits	Negative	Takele (2001)
1 improved variety	Grain amino acids content	Soil properties (P, Mg, Na)	Positive	Abewa et al. (2019)
1 improved variety	Grain crude fiber	Soil pH, Ca	Positive	Abewa et al. (2019)
1 improved variety	Grain color index of saturation	Soil properties (pH, C, Ca, Mg, and S)	Positive	Abewa et al. (2019)
36 improved varieties	Grain yield	NDF, ADF, ADL, SBM, STY	Positive	Jifar et al. (2018)
36 improved varieties	Grain yield	CP, ME, IVOMD	Negative	Jifar et al. (2018)
36 improved varieties	Crude protein	ME, IVOMD	Positive	Jifar et al. (2018)

RILs: Recombinant inbred lines; DH: Days to heading; DM: Days to maturity; GFP: Grain filling period; SB: Above ground biomass; PW: Panicle weight; PL: Panicle length; FT: Fertile tillers per plant; SPP: Number of spikelet per panicle; FPS: Number of floret per spikelet; KPS: Kernels per spikelet; PH: Plant height; CL: Culm length; NCI: Number of culm internodes; CD: Culm diameter; SCD: Second basal culm internode diameter; LI: Lodging index; HSW: Hundred seed weight; GY: Grain yield; HI: Harvest index; ELWL: Excised leaf water loss; RGR: Relative growth rate; SW: Shoot weight; RW: Root weight; CT: Culm thickness; RT: Root thickness; RSR: Root shoot ratio; RLD: Root length density; TN: Tiller number; LTP: Leaf turgor pressure; RGR: Relative growth rate; P: Phosphorus; Na: Sodium; S: Sulfur; Ca: Calcium; Mg: Manganese; C: Soil organic carbon; CP: Crude protein; NDF: Neutral detergent fiber; ADF: Acid detergent fiber; ADL: Acid detergent lignin; ME: Metabolic energy; IVOMD: In vitro organic matter digestibility; STY: Straw yield; PR: Pushing resistance; BS: Base failure moment

Fig. 3 Example specimens showing panicle type variability existing in the EBI teff collection. Photos taken in open field using white paper in the background to enhance contrast (Woldeyohannes et al. 2020)

is likely contributed by positive associations of plant height with panicle length (Jifar et al. 2015), thousand seed weight and harvest index (Tadele et al. 2013), days to maturity, culm length and diameter (Tefera et al. 2003). However, an increased plant height has not been a target for teff improvement, also due to its implications to lodging (Teklu and Tefera 2005). Biomass and particularly straw yield are priority traits for teff smallholder farming in Ethiopia, where straws are used for feed and house thatching (Jifar et al. 2018). When compared to barley straw, teff straw has a lower lignin content and higher quality for crude protein content, in vitro dry matter digestibility, and energy value (Yami 2013). In modern teff breeding, biomass increased at an average of 0.9% per year (Dargo et al. 2016) and showed that it may significantly contribute to enhance grain yield (Teklu and Tefera 2005). Plant vigour and production in teff can also be put in relation with root depth. Root traits in teff germplasm show wide genetic variation, including for root depth (59.3 to 116.5 cm), root number (18.3 to 72.8), and root shoot ratio (0.07 to 0.30) (Ayele et al. 2001). Increased root length may be associated with leaf turgor pressure under drought stress (Degu et al. 2008), as well as with salinity and acidity tolerances (Abate et al. 2013; Asfaw et al. 2011). Osmotic traits related to roots are also highly variable: in particular, osmotic adjustment (0.44 to 1.02 MPa), relative water content (97.8 to 99.5%) and osmotic potential (−0.88 to −1.15 MPa) (Ayele et al. 2001).

Seed traits

It is believed that the name teff derives from the Amharic word ጠፋ (Teffa) for *lost*, possibly referring to the remarkably tiny size of the seeds and the ease to lose them (Fig. 4). However, seed colour over seed size has been a target for teff breeding in the past decades, as colour is a primary trait for selection of grains in both formal and informal markets (Belay et al. 2008). Teff seed color varies from dark brown to white (Woldeyohannes et al. 2020), but white seeds fetch higher market prices and indeed most of teff varieties developed by breeding are white in colour (Table 4). Still, brown seeded teff genotypes are reportedly associated with aluminium toxicity tolerance (Abate et al. 2013), and may have higher nutritional content, supporting the need for their valorisation. Seed weight improvement did not result in a significant increase since the 1970s (Dargo et al. 2016). Though small overall, seed size is highly varied in teff collections, e.g. for grain length (0.9 to 1.7 mm) and thousand grain weight (0.19 to 0.42 g) (Assefa et al. 2001; Ebba 1975), suggesting untapped potential for improvement.

Phenology

Earliness is among the main teff adaptive mechanisms to prevent yield losses due to terminal drought. Possibly as a result of adaptation, teff accessions sampled in areas with lower rainfall have a shorter life cycle (Woldeyhannes et al. 2020). However, longer span of growth and later maturation are associated with increased yield and yield related traits (Tadele et al. 2013; Chanyalew et al. 2009; Tefera et al. 2003; Jifar et al. 2015; Assefa et al. 2002). In the EBI collection, a large variation exists for phenology traits: when evaluated in the same location, teff accessions mature with a span of 40 days from earliest to latest genotypes (Woldeyohannes et al. 2020). It is thus important that improvement for high grain yield should focus on maturity groups targeting different agroecologies.

Fig. 4 Contrasting seed colour of representative teff genotypes in the EBI collection

Leaf traits

Leaf traits are related to photosynthetic efficiency as well as to water balance in the plant. Leaf size in teff collections show large variation, including in flag leaf area (2 to 26 cm^2), leaf blade length (5 to 55 cm), and total leafiness of the plant (Ketema 1993; Ebba 1975). Across the genus *Eragrostis*, drought tolerance has been associated with increased leaf tensile properties (Balsamo et al. 2006). Tensile strength is higher in wild relatives than in *E. tef* (Balsamo et al. 2005, 2006), yet teff shows high variation for excised leaf water loss, drought deficit and leaf water potential, leaf relative water content and stomata conductance (Teferra et al. 2000). Differential responses to drought stress were observed among cultivars in association with leaf canopy temperature at anthesis, with higher temperatures associated to lower yields (Takele 2001).

Resistance to pests

Teff is regarded as relatively resistant to biotic stresses. Head smudge (*Helminthosporium miyakei* Nisikado) is arguably the most economically important disease in teff farming, and teff genotypes in collections showed some degree of resistance to it (Gemechu Degete 2021). No complete resistance is yet available for teff rust (*Uromyces eragrostidis* Tracy), another disease with broad diffusion in Ethiopia (Gemechu 2018; Badebo 2013). Teff rust typically occurs after heading stage, yet causes relatively little grain yield losses as compared to other constraints (Dawit and Andnew 2005). Resistance to aphids (*Rhopalosiphum padi*) is also available (Zafar et al. 2020), yet further evaluations are required to determine the status of genetic resistance alleles in teff germplasm collections.

Table 5 Selected micro and macro nutrient concentrations (mg/kg) of white seeded teff compared with brown seeded teff types

	Nutrient	White	Brown	References
Micronutrient	Copper (Cu)	2.5–5.3	1.1–3.6	Baye (2014)
	Iron (Fe)	9.5–37.7	11.6 to > 150	Baye (2014)
	Zinc (Zn)	2.4–6.8	2.3–6.7	Baye (2014)
Macronutrient	Calcium (Ca)	315	444	Dame (2020)
	Potassium (K)	1289	1147	Dame (2020)
	Magnesium (Mg)	543	437	Dame (2020)
	Phosphorus (P)	992	703	Dame (2020)

Nutritional features

Much of the national and international success of teff is due to its unique flavour and nutritional properties. Starch makes up about three-quarters of teff flour. Its amylose content (20 to 26%) is comparable to that of most cereals (Bultosa 2007), but the total dietary fibre content of whole grain teff (9.8%) is higher than that of major cereals and even higher than that of quinoa (7.1%)

Table 6 Valuable traits developed in mutagenized teff populations (Cannarozzi et al. 2018)

Trait	Background variety	Screening technique	Status
Drought tolerance	Tsedey and Dukem	Phenotypic screening	Drought-tolerant variety at the last stage of testing
Soil acidity tolerance	Tsedey	Phenotypic screening	Promising candidate obtained
Soil salinity tolerance	Kora	Phenotypic screening	Validation of candidates
Semi-dwarfism	Tsedey, Dukem and Kora	TILLING and phenotypic screening	Semi-dwarf and lodging tolerant variety to be released
Seed size	Tsedey and Kora	Phenotypic screening	Planned
Herbicide tolerance	Tsedey and Dukem	Phenotypic screening	Validation of candidates
Starch content	Tsedey	TILLING	Validation of candidates

(Gebru et al. 2020). Teff germplasm displays high variability in nutritional properties yet the highest iron and calcium contents are recorded in brown seeded varieties (Table 5) (Gebru et al. 2020; Yami 2013; Baye 2014). Fat (2% to 3%) and protein content (8% to 11%) in teff grain is similar, in some instances better, than that of other more common cereals (Moharram and Abu-foul 1992; Baye 2014), with a balanced amino acid composition and relatively high concentration of lysine (Ketema 1997). In teff flour, riboflavin ranges from 0.13 to 0.14 mg/100 g, niacin from 1.7 to 1.8 mg/100 g, and thiamine from 0.3 to 0.6 mg/100 g, higher than in most common cereals (Ketema 1997). Polyphenols and phytates are also present in high concentration (Baye 2014). This is also related to the fact that, due to its small size, the grain cannot be divided into germ, bran and endosperm during processing and it is consumed as a whole (Ketema 1997). The total phenolic content (mg GAE/gr) in teff ranges from 0.89–1.2 to 1.04–1.27 in white and brown grains, respectively (Tietel et al. 2020). Feed traits are associated with food quality traits and yield traits, confirming the possibility of improving feed quality traits without significantly affecting grain yield (Jifar et al. 2018).

Perspectives in teff breeding

The role of traditional knowledge

Smallholder farming is the most dominant form of agriculture in the Horn of Africa, contributing significantly to food security in the region. Teff is no exception. Smallholder teff growers accumulate and propagate indigenous knowledge that could be useful for a robust crop breeding program targeting local adaptation. In smallholder farming settings, traditional knowledge often drives selection and maintenance of germplasm for local adaptation (Fadda et al. 2020). In marginal cropping environments, farmer priority traits could be different from traits targeted by formal breeding objectives. Farmers' choice of varieties is indeed related to their desire to meet local economic, social and agroecological conditions (Ngonkeu et al. 2017; Mancini et al. 2017; Christinck et al. 2017; Fadda et al. 2020).

An integrated participatory characterization of crop genetic resource may be useful to design and address farmer preference traits in modern varieties to increase the adoption of genotypes and thereby increase productivity (Rahman et al. 2015; Ngonkeu et al. 2017), enhancing in situ conservation of indigenous knowledge. This approach has been reported in Ethiopian durum wheat accessions that showed the smallholder farmers' evaluation processes are quantifiable and repeatable (Mancini et al. 2017), and their knowledge can be harnessed in breeding programs (Kidane et al. 2017, 2019). In teff, preliminary results about farmer priority traits have been reported (Woldeyohannes et al. 2021), yet further research is required to fully translate this knowledge to breeding decisions.

Genetic variation and molecular breeding

Genetic variation is the raw material to fuel teff improvement. Although teff germplasm is highly diverse, some traits in the currently surveyed collections may still lack desirable variation, e.g. lodging tolerance (Assefa et al. 2013). Mutagenic agents may then be used to generate novel genetic variation from which desired individuals may be selected, and this approach was successfully used in teff (Cannarozzi et al. 2018). Among mutagenized teff lines, promising candidate lines were identified for seed size, herbicide tolerance, drought, soil acidity and salinity tolerance via subsequent phenotypic screening (Table 6).

Analyzing the molecular diversity encompassed in teff genetic resources is a prerequisite for their efficient exploitation in breeding and for the development of conservation strategies of its genetic diversity. In the past two decades, molecular markers technologies were used

Table 7 A selection of genomic and molecular studies performed on teff and related species in the last two decades

Main topic	Genetic materials	Approach	Practical implications	References
Genetic diversity in tef and its relatives	47 accessions of tef, three accessions of *E. pilosa*, and six accessions of *E.curvula*	RAPD markers	Genetic fingerprinting teff conservation and improvement	Bai et al. (2000)
Linkage map of teff	116 RILs from an inter-specific cross between tef cultivar *Kaye murri* and *E. pilosa*	RFLP markers	Characterization of the recombination landscape of teff and support for further genetic and genomic studies in teff improvement	Zhang et al. (2001)
Genetic diversity in teff	92 selected teff genotypes belonging to eight origin groups	ISSR markers	Genetic fingerprinting, teff conservation and breeding	Assefa et al. (2003)
QTL mapping of agronomic traits	124 teff F7 RILs	AFLP, ISSR, rice EST-SSR markers and tef specific EST-SSR markers	Useful information to enhance yield and yield related traits and lodging resistance	Chanyalew et al. (2005)
A genetic linkage map for teff and QTL mapping of agronomic traits	94 teff F9 RIL from an inter-specific cross between tef cultivar *Kaye murri* and *E. pilosa*	AFLPs, EST-SSRs, ISSRs, IFLPs and SNP markers	Useful information in marker assisted selection breeding to improve agronomic traits	Yu et al. (2006) Yu et al. (2007) Degu and Fujimura (2010)
Production and identification of semi-dwarf mutants	An EMS mutagenized population of 21,210 teff plants	High-throughput discovery of mutations using next generation sequencing of dwarfing candidate genes	Useful information to improve lodging resistance in teff	Zhu et al. (2012)
Genetic diversity in teff germplasm	326 cultivated tef accessions, 13 wild relatives, and four commercial tef varieties	SSR markers	Genetic fingerprinting for teff conservation and hybridization program	Zeid et al. (2012)
Identify mutations for genes responsible for agronomic and lodging tolerance traits	Teff cultivar Dukem (DZ-01-974) and teff cultivar Tsedey (DZ-Cr-37)	TILLING mutagenesis followed by high throughput mutation detection	Enhancement of lodging tolerance and agronomic traits in teff breeding	Korinna et al. (2013)
Transformation of tef by *Agrobacterium* with GA inactivating gene	Teff cultivar DZ-01-196	In vitro plant regeneration and detection of transgene insertion and expression	Genetic transformation in teff to induce dwarfism	Gebre et al. (2013)
Genome and transcriptome sequencing of teff	Teff cultivar Tseday	Genome and transcriptome sequencing	First genome sequence of teff	Cannarozzi et al. (2014)
Genetic relationship of teff genotypes	60 diverse teff genotypes	SSR markers	Genetic fingerprinting, teff conservation and breeding	Abraha et al. (2016)
Characterization of repetitive elements in the teff genome	Teff cultivar Enatite	Genome sequencing	Origin and evolution of teff transposable elements	Gebre et al. (2016)
Genetic diversity of teff and wild relatives	Landraces, improved varieties, and wild relatives	SSR markers	Genetic fingerprinting, teff conservation and breeding	Fikre et al. (2018)
Genetic relationship between teff and its wild *Eragrostis* progenitors	Landraces, improved varieties, mutant lines, and *Eragrostis spp.*	SNP markers	Genetic fingerprinting, teff conservation and breeding	Girma et al. (2018)
Identification of miRNAs linked with the drought response of teff	Teff cultivar Tseday (drought tolerant) and teff cultivar Alba (drought susceptible)	Genomic sequencing	Useful information for further genetic and genomic studies in teff breeding	(Martinelli et al. 2018)
Genome sequencing of *Eragrostis curvula*	*E. curvula* cv. Victoria	Genomic sequencing	Insights into Poaceae evolution	Carballo et al. (2019)
Genome sequencing of teff	Teff cultivar Dabbi (PI 524438)	Genomic sequencing	A high quality genome sequence of teff	VanBuren et al. (2020)
Genome wide association study for adaptation, agronomic traits, and farmer preferences	A collection of teff landraces representative of the EBI ex situ collection	SNP markers	The first GWAS in teff agronomic performance in relation to climate adaptation and farmers' preferences	Woldeyohannes et al. (2021)

RAPD: Random amplified polymorphic DNA; RFLP: Restriction fragment length polymorphisms; EST–SSR: Simple sequence repeats derived from expressed sequence tags; SNP: Single nucleotide polymorphism; INDEL: Insertion and deletion; IFLP: Intron fragment length polymorphism; ISSR: Inter-simple sequence repeat amplification; ISSR: Inter simple sequence repeat; RIL: Recombinant inbred line; TILLING: Targeting Induced Local Lesions IN Genomes; EBI: Ethiopian Biodiversity Insititute; GWAS: Genome-wide association study; QTL: Quantitative trai loci; EMS: Ethyl methanesulfonate to characterize the diversity of teff and related species in manifold studies (Table 7). Yet, advanced molecular breeding in teff has seen a very limited use as compared to other key cereals grown in Ethiopia (Girma et al. 2014, 2018; Teshome et al. 2020; Assefa et al. 2015). Most of teff priority traits highlighted above have not yet been exploited using modern molecular techniques. There is in general very limited information on high throughput discovery of single nucleotide polymorphisms (SNPs) and other molecular markers relative to *Eragrostis* species diversity with genomic based tools (Girma et al. 2018).

However, the accumulation of genomic information for teff (Cannarozzi et al. 2014; VanBuren et al. 2020; Woldeyohannes et al. 2021; Gebre et al. 2016) make teff ripe to be brought into the era of molecular breeding. Quantitative trait loci (QTL) have been described on teff for several traits including yield components and morphology (Chanyalew et al. 2005; Yu et al. 2007), also in relation to drought (Degu and Fujimura 2010). Recently, a large collection of teff landraces have been used to conduct a genome wide association study unveiling genomic loci potentially responsible for agronomic performance, climatic adaptation, and farmers' appreciation (Woldeyohannes et al. 2021). Once genes underlying QTL are discovered, genome editing may be used to enhance the agronomic performance of teff varieties. Efficient methods for transformation and regeneration of transgenic lines as those developed for cereal crops such as sorghum, maize, wheat, and rice (Numan et al. 2021) are needed before the potential of genome editing can be fulfilled in teff. However, early reports of transformation of teff to induce dwarfism suggest that efficient transformation protocols may be achieved also in this species (Gebre et al. 2013). In rice, the editing of a handful of genes involved in yield determination generated mutants with increased grain number, tiller number, dense erect panicles and large grain size and plant architecture (Rakshit et al. 2020). Similarly, panicle architecture may be edited to generate tiller spreading phenotype enhancing crop yield in rice (Zafar et al. 2020), suggesting similar applications for teff breeding.

Conclusion

Teff breeding is approaching a golden age contributed by the emergence of knowledge and tools deriving from its vast and untapped diversity. In Ethiopia, teff breeding may be conducted with two generations per year. Even so, more than 10 years are required today to develop and release an improved teff variety using hybridization (Chanyalew et al. 2019). Genomic innovations supporting molecular breeding may be put at use with alternative breeding methods including speed breeding (Chiurugwi et al. 2019; Watson et al. 2018) and 3D-breeding (van Etten et al. 2019; de Sousa et al. 2021) to speed up the development of teff varieties with enhanced local adaptation and farmers' uptake. The enhancement of teff productivity, nutritional quality, and farmer appreciation may leverage the great diversity existing in teff collections and use modern molecular tools to open a new era of teff breeding. The appropriate combination of this wealth of information is needed to revolutionize teff cropping and propel it towards the international market.

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