In depth field characterization of Teff [*Eragrostis tef (Zucc.)Trotter*] variation: from agronomic to sensory traits

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Abstract

A diverse collection of Teff [*Eragrostis tef (Zucc.)Trotter]* lines was characterized for a wide range of traits, ranging from agronomic to final Injera sensory parameters, under well-irrigated Mediterranean spring conditions. The lines tested were collected from single plants presenting lodging resistance at the site of collection and their traits were characterized herein. An early type of lodging was observed, which was most likely triggered by a fast and sharp inflorescence weight increase. Other lines were 'strong' enough to carry the inflorescence most of the grain-filling period, up to a point where strong lodging occurred and plants where totally bent to the ground. Three mixed color seeds lines were found at single plant collection or after propagation. These were separated into 'white' and 'brown' seeds and were characterized separately under field conditions. The newly 'brown' lines appear to be the result of a rather recent non-self (external) airborne fertilization from a dark pollen donor. Some of these hybrids were found to be promising in terms of Injera sensory traits. Integration between a wide range of parameters and the correlations obtained between agronomic and sensory traits may improve our ability to breed towards a "real world" better end-product.

Keywords

Crop breeding, Lodging-resistance, Teff [*Eragrostis tef (Zucc.)Trotter*], Injera, Sensory evaluation, productivity, Chlorophyll

Abbreviations

AGW (Average Grain Weight), gr

Chl a/b ratio

Chl/gFW (Total Chlorophyll / gram Fresh Weight)

Chla/gFW (Chlorophyll a/ gr Fresh Weight)

Chlb/gFW (Chlorophyll b/ gr Fresh Weight)

DAS (Days After Sowing), days

DPM (Days from Panicle emergence to Maturation)

DSM (Days from Sowing to Maturation)

DSP (Days from Sowing to Panicle emergence),

DT<75% (Days to reach 75% of the plants lodging in a plot)

EGC (Early Ground Cover), %

GY (Grain Yield), kg/plot

HI (Harvest Index)

LSD (Lower Stem width), cm

MPH (Maximal Plot Height), cm

SL (Seed length), µm

SpL (Spikelet length), µm

TDM (Total Dry Matter), kg/plot

USD (Upper stem width), cm

Introduction

Tef [*Eragrostis tef* (Zucc.) Trotter], commonly referred to as Teff, is an annual self-pollinated, allotetraploid (2n=4x=40) warm season crop belonging to the Poaceae (grass) family (Assefa et al., 2015, Costanza et al., 1979). It is a major food crop native to Ethiopia and Eritrea for the production of a range of traditional foods and beverages including Injera (flatbread).

Teff is a C_4 plant which has high chlorophyll a/b ratios and utilizes CO_2 very efficiently during photosynthesis. Teff is adapted to a range of growing environmental conditions (Kebede et al., 1989). Teff grain also presents excellent storage properties. Therefore, it plays an important role in food security in eastern Africa and in combating global climate change (Zhu, 2018).

In recent years, Teff is becoming popular in the health-food markets of developed countries due to its attractive nutritional properties and gluten free nature. The inability to separate the bran from the seed makes Teff flour rich in fiber and thua has health benefits as an anti-oxidative and improves Hemoglobin level in the human body (Zhu, 2018, Berhe, 2018).

Despite Teff's versatility in adapting to extreme environmental conditions, Teff is susceptible to lodging, which can drastically reduce yield and grain quality, and complicates harvesting (Berhe, 2018). Lodging can limit productivity directly by reducing photosynthetic capacity due to changes in sun/shade architecture. Lodging also limits the use of high input Nitrogen fertilizer to boost yield.

Lodging is a process by which the shoots cereals are displaced from vertical orientation (upright position) and settle in a permanent horizontal position (Berry et al., 2004). It is a complicated phenomenon that is influenced by many factors including wind, rain, geography, landscaping, soil type, crop history, agricultural system and disease (Berhe, 2018).

Stem lodging results from bending or breaking of the lower culm internodes, and root lodging results from a failure in root soil integrity (Sterling, et al., 2003). The problems of lodging can be reduced by decreasing plant height, however, yield is reduced when plants are shortened too much with dwarfing genes or plant growth regulators (Berhe, 2018). Hence, it was suggested to target other traits than height for further improvement in lodging resistance.

Teff has weak stems that easily succumb to lodging caused by wind or rain (Assefa, 2015). Various attempts have been made to develop lodging-resistant Teff cultivars but presently no cultivar with reasonable lodging resistance has been obtained (Assefa et al., 2011, Assefa, 2015). Despite lodging being the greatest cause for yield loss in Teff, its genetic and physiological control is undertaken by molecular breeding techniques and biotechnology (Berhe, 2018).

A lodging index can be computed as a weighted average lodging scores according to a 0-5 scale.

Caldicott and Nuttall method (Caldicott et al., 1979) calculates the index as follows: Lodging index = [Sum (lodging score × the relative area for the score)] / 5.

Ethiopia is Teff's origin and the center of its biodiversity, harboring landraces with a wide array of phenotypic diversity, and wild progenitors and related wild species. The genetic diversity of Teff is represented in a collection of over 5,000 accessions (reviewed by Assefa et al., 2015) at the Ethiopian Institute of Biodiversity. There has been major increase in the collection size over the last decades which demonstrates the presence of both a wide diversity of germplasm in Ethiopia, as well as the commitment of institutes and individuals to collect and preserve these germplasms for future use (Assefa et al., 2015).

The genetic diversity in Teff was also discovered by using a range of molecular markers (Zhu, 2018) and its genome has been sequenced (Cannarozzi et al., 2014). Great genetic diversity in yield, lodging index and stem strength related traits has been recorded in Teff (Zeid et al., 2012).

Phenotypic variability in Teff was recorded in: grain yield, grain color and size, days to panicle emergence, days to maturity (21 to 81 and 50 to 140, respectively), number of grains/plant (9,000–90,000), plant height (20–156 cm), number of tillers/plant (5–35), and culm diameter (1.2–5 mm; Assefa et al., 2001 a and b).

Teff breeding should target the improvement in the following traits: grain yield, shoot biomass, lodging resistance, grain size and color, grain coat properties, nitrogen-use efficiency, osmotic adjustment root depth, tolerance to drought, salinity, and acidity, nutritional, physicochemical, and palatability (Assefa et al., 2015). Variability for culm internode diameter is a key factor for improved lodging resistance (Zhu, 2018).

Overall, there is a limited amount of research on the genetic basis for processing, palatability, and nutritional quality of Teff and its components as food (Zeid et al., 2011). Teff variety may greatly affect the processing, palatability, and nutritional quality of food products. Therefore, it is necessary to assess the genetic diversity of this crop for potential improvement of agronomic as well as food processing traits (Zhu, 2018).

The preparation of Injera, the Ethiopian sour-dough type flat bread, involves fermentation processes of the Teff flour (Ketema, 1993). The fermentation preparation consists of two stages of natural fermentation, which last for about 24 to 72 hours, depending on ambient temperatures (Gamboa, 2008). Good quality Injera will have uniformly spaced honeycomb-like "eyes" or holes, and no blind spot (flat area with no holes) on its surface. The major factor that decrease Injera quality result from inadequate fermentation. Good quality Injera becomes soft and pliable in texture, which enables the consumer to wrap and pick up sauce in the Injera with fingers (Berhe, 2018). In Ethiopia, people prefer their Injera to be white (Berhe, 2018). Texture is determined by touch and refers to the degree of fluffiness, roughness, smoothness, hardness or softness.

Results from the six crosses of parental lines differing in lemma color (purple, red grey, and yellowish-white), show that at least four pairs of genes control the inheritance of lemma color in Teff (Berhe, 2001) with dominance complementary and epistatic gene actions. Berhe, (2001) suggested the following model: C is a gene for basic anthocyanin color; P1 and P2 are duplicate genes responsible for development of purple lemma color in the presence of dominant C (Either P1 or P2 alone); p1 and p2 are genes responsible for red lemma color in the presence of dominant C; G is gene for gray lemma color visible only when dominant C is absent; g is gene for yellowish-white lemma color in the absence of C and G (Berhe, 2001).

Four phenotypes of seed coat color (grain color) were documented in Teff: dark brown, medium brown, yellowish-white, grayish-white. However, the dark and medium brown are difficult to differentiate so they are both included as brown. A duplicate gene pair is known to be involved in seed color inheritance, with simple dominance and additive gene effects. Tests of independence showed that lemma and seed color are inherited independently (Berhe, 2001).

There is scarce documentation on seed size and seed coat in Teff (Assefa et al., 2015). Depending on the varieties, the color of Teff grain can be ivory, light tan to deep brown or dark reddish-brown to purple (Assefa et al., 2015, Berhe et al., 2018). Based on people's preference for their consumption, white Teff is the most expensive, while in terms of beneficially red Teff is more nutritious and gains acceptance by the health-oriented consumers in Ethiopia and worldwide (Berhe et al., 2018).

Different Teff varieties have different mineral concentrations. Red Teff has a higher content of iron and calcium than mixed or white Teff varieties, and in contrast, white Teff has a higher copper content than the red and mixed Teff varieties (Berhe et al., 2018).

In Israel, there is a growing interest in Teff and there is a significant Ethiopian community which is involved in the preservation of seed resources. Several community experimental gardens exist, and the Israeli seed bank holds a large collection of Teff lines (Ben-Zeev et al., 2018).

In a Teff plot we found plants that looked different from the surrounding population. First, and most striking, was the lodging resistance presented by these single plants under the prevailing environmental conditions compared to the surrounding plants. Secondly, these plants, randomly distributed within the plot, were different from the common white cultivar in stem diameter, leaf size, phenology and inflorescence coloration. From each of these plants a single panicle was collected for further characterization.

The objective of this study was to characterize this newly discovered source of diversity in terms of lodging, agronomic and sensory traits.

Materials and methods

Plant Material

Thirteen Teff lines that were found among white Teff plot were analyzed. These randomly distributed plants looked different from the general population in terms of lodging (Fig S1). A single panicle was collected from 13 of these plants for further study. These lines were propagated off-season in a greenhouse (Fig S2), and from them 11 lines were selected for further detailed analyses under field conditions. These included (Some are detailed in Table 1): 44A-163-B (pure brown) and 44B-163-W (pure white). The three lines: 53-1, 53-2 and 53-3 were also included, and were found to be a mixed color after a generation of propagation (excluding 53-1 which was already mixed when collected) as detailed in Table 1. Each of the three exhibited a different proportion of brown/white seeds after one cycle of propagation (Table 1), threshed as a bulk, and then separated into white and brown manually. We also harvested two plants separately from the greenhouse pot of 53-2 in order to establish a single plant selection according to lodging resistance score, to create 53-2-1-W and 53-2-2-W. As a control we used one of a commercially grown cultivars in Israel, refereed herein as the 'white cultivar'.

Pot propagation and phenotyping

Seeds from a single plant for each of the lines were sowed in small pots in the first stage (August 2018), and then transplanted into 10L pots in a greenhouse (*31°55'45.23" N 34°51'56.27" E*) located at ARO, Bet Dagan, Israel. Pots were well irrigated using a dripping system (Fig. S2).

Although statistics were unavailable during this propagation cycle due to the small number of plants, several traits were scored per pot (Table 1). Maximal plant height (MPH) was measured from the pot surface to the top of the panicle. Grain was threshed manually and grain yield (GY) was measured in dry weight (gr) per pot. Stems were counted for each pot and grain per stem was calculated. Days from sowing to panicle emergence (DSP) was evaluated as the date over 50% of the plants in the pot were at or after panicle emergence. Plants where harvested at maturity, weighed and threshed manually. Average grain weight was roughly assessed by the calculation of the mean value of 10 seeds.

Field trial

A total of eleven lines (Table 1) were subjected to a field trial within the growing season under well-irrigated conditions. The trial was held at the ARO located at Bet Dagan, Israel. Seeds that were propagated in the greenhouse were sown at March 7th, 2019, where each experimental unit was comprised of a 0.9m x 2m plot (Fig. S3). Raised beds were implemented and irrigation and fertilizer were applied using a dripping system. Most lines had between 3-5 replicate plots , except for the brown lines 53-1-B, 53-2-B and 53-3-B because their seed yield was insufficient for more than a single replication. Seeds for each plot were sown in a row alongside the dripping system in six rows. Seeds for each row were placed within a tube which was used to

evenly distribute the seeds between rows. These seeds were weighed in advanced and were sown at a rate of 2.4 gr per 1.8m^2 plot as a base line. Since AGW was different between lines, this proportion was used to standardize seeding rates (relative to the white cultivar) for each line. Express® herbicide was applied (0.1% with BB-5) 13 days after sowing (DAS), when the plants emerged .

Phenotypic measurements

Total dry biomass and grain yield

At full grain maturity and after plants were fully dried, all aboveground biomass was harvested and weighed to determine total dry matter (TDM) for each plot. Grain was then threshed using Wintersteiger thresher apparatus. Grain was weighed to determine grain yield per plot (GY) and Harvest index (HI) was calculated as the ratio between GY and TDM.

Early Ground Cover

Early growth cover (EGC%) was measured at 33 DAS. *CoverageTool*(Merchuk et al., 2019) was used to quantify ground coverage by canopy in percent for each plot. A set of photos was taken vertically from above the plots under the same settings (height of camera from the ground, light, same camera, Fig S4). Then, the canopy colors were sampled to be taken into account (foreground), whereas the bare soil brown shades were not selected (background).

Chlorophyll

Chlorophyll a and b were measured at 42 DAS, from the youngest fully extended leaf blade. Leaf samples were weighed and then placed in DMF for 72 h. Absorbance of the extracted pigments was measured using a spectrophotometer (UV-VIS recording spectrophotometer, UV-2401PC) at 645nm and 663nm. The photosynthetic pigment content was expressed in mg per gram-fresh weight leaf tissue (mg/g-1 FW), as adapted from (Kolotilin et al., 2007).

Stem width

Stem width projection was measured at 70 DAS (at or after stem elongation phase, Fig. S5) for the first lowest node which bears one leaf (upper) and, the most basal internode (lower, below Fig. S5).

Phenology

Days from sowing to panicle emergence (DSP) was recorded based on daily inspection and was evaluated as the date over 50% of the plants in the plot were at/after panicle emergence. Days from panicle emergence to maturity (DPM) was recorded at maturity (upon plants desiccation). Days from sowing to maturity (DSM) was recorded as well.

Average Grain Weight

Average grain weight (AGW) was measured by first weighing the seeds (˜60mg). Next, these seeds were spread over a white sheet and photographed. For each plot the image was threshold using '*coveragetool*' (by sampling seeds to account, Fig S6). Then, the threshold images were analyzed using Image J's 'particle count' option. Finally, AGW was calculated as the seed weight divided by number of seed for each plot.

Seed length and Spikelet imaging

Seed length was measured using a Leica MZFLIII fluorescence stereomicroscope. About 12 seeds were measured for each plot, and the mean value was recorded. Spikelet images for each line were recorded using Leica MZFLIII stereomicroscope as well.

Height dynamics Average plant height in each plot was measured from 53 DAS up to 77 DAS (eight times). Height (H) was measured at three different locations along the plot, from the ground up to maximal plant height (which could not be absolutely defined as the panicle tips). As panicles emerged (and during grain

filling) the fraction of the plot which exhibited lodging was scored (F), as well as the height of the lodged fraction (LH). p Plant heights were averaged as follows:

Avg plot plant height = (Erect fraction * H) + (Lodged fraction * LH)

Maximal plot height (MPH) was the maximal height the plot had reached, regardless of the lodging fractions.

Injera Sensory Trial

In this experiment we used bulked grain samples (from our ARO field trail) from each line. These samples were passed through a 0.85mm sieve (U.S.A. standard test sieve, Fisher Scientific Company) and grain were further cleaned using the Selecta machine (Machinefabriek BV. Enkhizen- Holland). The samples were then ground to flour by Pashut (https://www.pashutli.co.il/) grinding services, which can grind relatively small grain samples (300gr in our case), followed by a final manual sieving through a kitchen sieve. Within a week from grinding, sensory evaluation was conducted and the flour was stored in sealed plastic bags at 4degC.

A total of 14 flour samples including from the 11 lines grown in the ARO field experiment with additional three samples bought in local markets (two white and one brown flour samples) were included in the test. The flow diagram of Injera preparation is described in Fig. 1.

We were kindly assisted by Mrs. and Mr. Leute in the Injera sensory trial preparation. All Injera flat bread were prepared similarly, using the same quantities, proportions and apparatus. The sensory evaluation was conducted 8 hours after baking the Injera. In this study, a panel of 14 Ethiopian judges (eight males and six females, 27-73 years old) was used to assess the degree of consumer acceptance/satisfaction on the Injera prepared from the different lines and controls. The judges were requested to taste the samples and rate various characteristics on a five-point scale (1- "Strongly dislike"/lowest, and 5- "Like very much"/highest). The traits that were evaluated were (Table 2): general appearance, color (color preference), odor (odor preference), odor intensity (odor strength), texture (softness), acidity (strength) and flavor (taste preference).

Statistics

The JMP version 12.0 statistical package (SAS Institute, Cary, NC, USA) was used for all statistical analyses.

Results

Off season phenotyping and line segregation

The subjected Teff lines were propagated in 10L pots in the greenhouse off-season. Each line originated from a single panicle of a single plant. The initial collected seed set AGW (0.23-0.60 mg) as well as AGW scored from the greenhouse (0.22-0.50 mg) are presented in Table 1. MPH ranged from 147 to 200 cm. The white cultivar and the pure brown cultivar 44A-163-B presented similar heights. The white cultivar had more stems per pot and panicle emergence was about a week earlier than the rest of the lines under these condition.

Three lines that had mixed color seeds were separated as detailed in Table 1. The proportion between the brown to white seeds was tripled from 0.021 to 0.064 within a generation of prorogation. Whereas in 53-2 and 53-3 no dark brown seed were detected upon collection. However, after second round of propagation in the field dark brown seed were found in those lines (0.105 and 0.015 for 53-2 and 53-3 respectively).

Phenotyping

Analysis of variation for most traits showed a significant line effect (ANOVA in Tables 3-8). Within the agronomic and plant physiological parameters tested, a very wide range of values was found for EGC and Chlb/gFW (higher than 3 folds, Tables 3 and 4). A medium range (2-3 folds) was recorded for: TDM, GY, HI, LSD, Chla/gFW, Chl/gFW, Chl a/b ratio, and AGW. A low range of values (under 2 folds) was found for: USD, DSP, DPM, DSM, SL and MPH. ANOVA analyses of all of the sensory traits (except for 'Odor intensity') reveled a significant effect of variations between the lines (Tables 9-10).

Biomass production

A range of GY was observed in the current study. The white commercial cultivar and pure brown 44A-163-B were ranked relatively high in GY and HI and low in TDM, with the former showing a significantly higher GY as compare to the latter (Table 3). Interestingly, the brown lines (53-1-B, 53-2-B, and 53-3-B) exhibited a similar pattern and were also ranked higher in GY and HI and lower in TDM as compare to most of their white counterparts (Table 3). The best preforming in terms of GY was the white cultivar. Second was 44B-163-W, which was not significantly different from the pure brown 44A-163-B, as well as from the other brown lines

Early growth cover and Chlorophyll measurements

Early growth cover (Table 4 and Sup Fig .4) of the white commercial cultivar and 53-3-B was low as compared to other lines (such as 53-1-W) at 33 DAS. 53-1-B and 53-2-B exhibited the highest values of EGC.

Leaf chlorophyll content was measured at 42 DAS (a, b, and total Chl). Both the commercial white cultivar and pure brown 44A-163-B line had a very similar midrange value (Table 5). Both 53-3-B and 53-1-B contained the highest Chl (b, and total Chl) among the evaluated lines. Whereas 53-2-B exhibited the opposite patterns in terms of Chl levels. Interestingly, all three brown lines presented a low Chla/Chlb ratio.

Phenology

The difference in panicle emergence time ranged between 53 to 64 DAS the white commercial cultivar being the earliest to enter the reproductive stage at 53 DAS (Table 6), along with 53-1-B. In general, the brown lines exhibited earlier heading compared to their white-counterparts. 53-3-W was the latest to head and had the highest DSP, DPM and DSM within the collection. While the white commercial cultivar was significantly earlier than brown 44A-163-B, their grain filling period (indicated by DPM) was not statistically different. Both the pure brown 44A-163-B and the white cultivar exhibited the lowest DSM in the collection.

Stem phenotyping

Stem width was measured at 70 DAS during stem elongation and the lower and upper basal stem widths were measured (Table 4). The brown lines (as well as the white commercial cultivar) tend to group as having a narrower stem (low USD and LSD) than the white lines (Table 4). The single plant selected 53-2-2-W exhibited the highest LSD in the collection.

Plot plant height dynamics and lodging

Maximal plot plant height of the white commercial cultivar and two of the brown lines: 53-1-B and 53-2-B, was lower compared to the other white lines (Table 8). The dynamics of plant height, which was documented in detail from 53 DAS to 87 DAS (Fig. 2 and 7, Table 8), revealed distinct patterns among the studied lines.

The white commercial cultivar was the first to enter the reproductive stage at 53 DAS. The white commercial cultivar started exhibiting lodging three days after panicle emergence. However, this lodging was later revealed to be essentially different from the lodging observed in other lines. The main differences were that while the white commercial cultivar was relatively uniform in its lodging across the plot (Fig. S8a), as well as relatively static/stable in terms of plot's height throughout the grain filling period (at around 35cm above ground); the other lines did not lodged so soon after panicle emergence and their lodging was not uniform across the plot. For example line 44A-163-B started lodging between 70-77 DAS (Fig. 2, Fig. S8b), and plot's height reaches around 50cm above ground. Other lines, such as 44-B-163-W exhibited strong lodging between 70 and 77 going from plot height of 77 cm to 27cm in seven days (Fig. S8c). This line was among the tallest lines and its heavy panicles filling seemed to bend the entire plant downwards. Some of the lines, such as 53-2-2-W, exhibited a relatively prolonged period of erect posture during grain filling, before lodging (Fig. S8d) which was not severe.

Seed and Spikelet phenotyping

AGW of the brown segregated lines 53-1-B and 53-3-B was significantly higher as compared to their white counterparts (Table 7). The commercial cultivar exhibited midrange values of AGW. Similar pattern was

obtained for SL, where this time all three brown segregated lines exhibited significantly higher averaged values as compared to their white counterparts (Table 7).

Coloration of the Spikelet lemma was also documented (Fig. 3). The white commercial cultivar lemma were gray-purplish and highly transparent. 44A-163-B exhibited a dark-purple coloration and was transparent as well. 44B-163-W exhibited bright pink lemma with whitish-gray outer borders and veins. The brown seeded line of 53-1 exhibited much less pink coloration (mainly at the outer borders) compared to their white counterparts, which had bright pink lemma with white gray outer borders and veins. The second brown line of 53-2 exhibited purple coloration at the outer border of the lemma as compared to their white counterparts which were pink - not purple. The third brown line of 53-3 also exhibited purple coloration at the outer borders of the lemma as compared to the white counterparts, which had whitish-gray lemma (similar to the white cultivar in terms of coloration).

Injera sensory evaluation

The sensory evaluation acceptability trials of Injera made from 14 flours samples of the 11 lines grown in the ARO field experiment with additional three commercial samples bought in local markets are presented in Table 9 and Table 10 and Figure 4.

The sensory evaluation scored values for all sensory attributes were sampled 8 hours after baking the Injera by a panel of 14 Ethiopian judges to assess the degree of consumer acceptance of Injera prepared from different lines.

44B-163-W and 53-3-B were significantly preferable in terms of Injera appearance, color and odor, which significantly differed from some of the lines, but not from the commercial ones. In terms of Injera appearance, color and odor, 53-2-1-W was significantly the least preferable. 53-2-1-W also presented the highest (unpleasant) odor intensity compared to 44A-163-B, which had the lowest odor intensity.

Both 44B-163-W and 53-3-B exhibited a relativity low odor intensity (which is apparently preferable). The texture of all market samples as well as that of the white cultivar was generally ranked higher than the rest of the lines. The acidity level of 53-2-2-W was the highest among the collection while the market samples were generally less acidic in taste The highest ranked in terms of flavor were 53-3-B, 44A-163-B (around 3.2), and the lowest were 53-2-B and 53-2-1-W (around 1.6),.

Correlations

Table 11 shows the correlation matrix obtained for the studied traits. TDM was found to be significantly negatively correlated with: Chlb/gFW (r=-0.8**), Chl/gFW (-0.71**), and positively with USD (0.79**) and LSD (0.63*). GY was negatively correlated with MPH (-0.8**) and with LSD (0.63*). The correlation between Chla/gFW and Chlb/gFW was found strongly significant (0.88***). MPH was correlated with TDM, USD and LSD (0.66*, 0.68* and 0.74**).

Low DSM or DSP were correlate with increased GY (r=-0.62* and -0.69* respectively), and SL (-0.65* and -0.63*).

In the sensory parameters evaluated, flavor was found to be positively correlated with odor (0.9***) and color (0.7*), and negatively with odor intensity (-0.86***). Odor and odor intensity were negatively correlated (-0.86***), and color and appearance were positively correlated (0.90***). Odor and color were positively correlated (0.7*).

Flavor was positively correlated to Chlb/gFW (0.6*) and negatively with TDM (-0.61*) and USD (-0.64*). AGW was found to be positively correlated with odor intensity and negatively with acidity (-0.73***). Texture was found negatively correlated (-0.64*) with USD, and USD was positively correlated with odor intensity.

Principal component analysis

Principal component analysis (PCA) for all studied traits was conducted (Fig. 5). PCA was based on a correlation matrix and presented as bi-plot ordinations of RILs (PC scores). Two components were extracted using eigenvalues > 1 to ensure meaningful implementation of the data by each factor. The PCA of the 11 lines extracted two major principal components (eigenvalues > 1) that accounted collectively for 56% of the variance between the lines. Principal component 1 (PC1, X -axis) explained 37% of the data set variation, and PC2 (Y -axis) explained 19% of the data set variation.

Both the correlations and the PCA showed a negative association between the two components representing reproductive variables (GY and HI) and: MPH, DSP, DSM, DT<75%, LSD (r=-0.8**, -0.69*, -0.62*, -0.64* with GY respectively). Along that axis of association the white commercial cultivar as well as the brown segregants are the highest yielding and lowest MPH, DSP, DSM, DT<75%, LSD.

Injera color and appearance were grouped and were negatively associated (r=-0.61*) with EGC. Another group which was obtained was negatively associated with TDM and odor intensity, which included the traits: Chl Tot, Chlb, flavor and AGW (r=-0.71*,-0.8**,-0.6*, -0.64*, with TDM respectively).

Discussion

The Teff lines evaluated in this study exhibited a wide phenotypic variation (Supp. Fig.7a), which is comparable to previous literature reports (Assefa et al., 2002, Girma et al., 2019, Nigu el al., 2016). For example, the GY range in the current field experiment was equivalent to 0.24-0.6 t/ha, where the national average farmer's yield is around 1 t/ha, and 2.5 t/ha under experimental conditions in Ethiopia (Berhe et al., 2011, Girma et al., 2019, Nigu et al., 2016, Zhu, 2018). Teff has a potential for yielding 4.6-5 t/ha if lodging can to be resolved (Hailu et. al., 2000). Harvest Index values previously reported (Assfa et al., 2002) were of a similar range to our field experiment (Table 3). In addition, phenological values (Table. 6) were in accordance with previously reported ranges for Teff cultivation (Assfa 2001 b & 2002).

Within the genetic material tested, no correlation was found between TDM and GY, whereas in other reported positive (Braha et al , 2017) or negative correlation (Chanyalew et al., 2010, Lule & Mengistu, 2014). However, when analyzing the white and brown separately (and excluding the white cultivar which appears to be much different) there appears to be some degree of correlation (r=0.6 and 0.7 for the white and black respectively), yet not statistically significant. We found correlation between GY and HI (0.8***) that was in agreement with previous reports (Lule & Mengistu, 2014).

Plant height was previously reported to range between 74 and 116 cm (Assfa, 2002). Under our field conditions, within the growing season MPH was 58-78 cm (Table. 8), and in the greenhouse off-season MPH was 180-200 cm (Table 1), which was more than double field growth but with narrower range across the lines. Differences in day length and other environmental factors may account for these differnces. Some of the lines were ranked similarly in both experiments (Table 1 and 6) in terms of MPH.

Since there are two duplicate genes for grain color in Teff, which are known to be dominant (Berhe et al., 2001), the small fraction of the brown seeds found within the seeds propagated from the initial collected panicle (0.064, 0.105 and 0.015 for 53-1, 53-2, 53-3 respectively, Table 1, Fig. 6) can only be explained by an external foreign pollination. The increase in brown seed ratio in 53-1 from the first collected generation to the greenhouse next-generation, from 0.021 to 0.064 - as would be expected from the segregation of o heterozygosity of the grain color loci (A/a). The small fraction of A/a in the collected panicle would be expected to triple (a total of: 1 A/A and 2 A/a) over the course of a single generation. The data also support the hypothesis that the brown lines are half-siblings (hybrids) to their white counterparts; these half-siblings share the maternal side but differ in the paternal one. It is very likely that these hybridizations were most probably wind-driven. As oppose to 53-1 No dark brown seeds could be detected within the grain of the collected panicles of these two lines, so there must have been undetectable light brown seeds that were in a heterozygous state A/a and were later segregated.

The brown lines in this study (pure and segregating) exhibited an overall advantage over the white lines in terms of directing their biomass towards grain production (Table 3, PCA Fig. 5, excluding the case of the

'white commercial cultivar'). The white commercial cultivar, the pure brown 44A-163-B and some of the segregating brown lines were the highest ranked for GY (Table 3, PCA Fig. 5).

A clear pattern emerges that all brown hybrids being earlier to flower (along with the white commercial cultivar, Table. 6) as compare to their white half-siblings. Therefore, it is possible that the pollen donor/s was/were a relatively early flowering type . Also the significant differences in plant height, observed between 53-2-W and 53-2-B (76 cm vs. 58 cm, Table 7) may indicate that the pollen donor in this case has a shorter stature than the maternal line.

53-3-B, which originated from the segregation of the mixed color line 53-3 into brown and white seeds (Table 1), was especially interesting. This line exhibited relatively low TDM and high HI (Table 3), low EGC (Table 4), and high Chl levels (Table 5). Contrastingly, this line was also relatively tall as indicated by its high MPH (Table 7) and thin stems (Table 4). In terms of sensory evaluation, 53-3-B was the most promising line with its preferable taste, smell and appearance (Tables 9 and 10).

Our hypothesis is that each of the three half-siblings originated from a different pollen donor was strengthened by the large variations in Chl levels between the three half-siblings. 53-2-B had the lowest Chl levels, and 53-1-B and 53-3-B exhibited the highest levels among the collection (Table 6 and Fig. 3). Interestingly, 53-2 which presented the lowest Chl levels had the highest GY among the three. Another result was the grouping of the traits: Chl Tot, Chlb, flavor and AGW that was negatively correlated with TDM (Fig. 5). This is in agreement with the literature that suggests that a smaller plant may contain denser leaves and more chloroplast and Chl per gr FW of leaf tissue (Fritschi & Ray., 2007). The positive correlation obtained between flavor and Chl may be indirect however, these correlations may have importance for future breeding programs as initial phenotypes for selection.

Following the genetic model of lemma color (Berhe et al., 2001), it appears that both the maternal line of 53-2 and 53-3 had the basic p1 and/or p2 genes in the background of the dominant C gene thus resulting in red lemma color, and that the hybridization with an unknown brown donor introduced a P1 or P2 thus resulting in purple lemma color. There seems to be differences that may have come from maternal differences between 53-2 and 53-3 in lemma color, because 53-3-W was not red as 53-2-W, but rather gray (Fig. 3).

In this work we characterize in detail the lodging phenomena in the studied Teff lines. The simplified scoring system for lodging (Caldicott & Nuttall, 1979), which is commonly used, does not take into account at which growth stage lodging starts nor the uniformity of lodging within a plot. Therefore we choose to document plot-height over the course of the reproductive period (Fig. 2), as well as to calculate the days to 75% lodging in a plot. This detailed inspection and documentation explains mechanisms related to Teff lodging (Fig. 2 & Supp. Fig. 7-8), which are very much context-dependent in terms of environmental conditions. In that respect, the lodging resistance which was the reason for collecting these lines to begin with, (Supp. Fig. 1). It appears that since the collected plants growing randomly as single plants within a homogeneous lodging inclined genetic population as well as occurring at very low-density planted areas, showed a lodging-resistant phenotype. In well-irrigated, well fertilized and low-stress conditions of our experiments, completely lodging-resistant line was not found, and lodging seems to be a flash-mob phenomenon were several plants start a lodging movement that sweeps the reset of the field. However, we show that our in-depth documentation and interpretation of lodging here may be useful for future breeding of -lodging resistance characteristics in Teff.

High yielding lines tend to lodge at harvest time (Yu et al., 2007, Davison & Laca, 2010). The lack of variation in lodging resistance may be a result of unfavorable associations of lodging resistance with productivity promoting traits such as plant height, panicle length, grain and shoot biomass (Kebebew et al., 2011, Nigus Eet al., 2016, Yu et al., 2007). Improvement of lodging related traits, such as culm length, overall-height and diameter of the culm internodes, through breeding is expected to be a demanding task due to their relatively low heritability and lack of reliable genetic advance-estimates (Assefa et al., 2001a). Therefore, increasing our understanding of the lodging phenomena and its phenotyping can improve our ability to breed for high yielding lodging-resistant cultivars. This study shows that the nature of lodging is variable in terms

of timing and strength (Fig. S7a). In terms of timing, we observed an early type of lodging which was most likely triggered by the fast inflorescence weight increase exhibited by the white commercial cultivar (Fig. 3 and Fig. S7b) and 53-1-B (Fig. 3). Other lines were 'strong' enough to carry the inflorescence most of the grain-filling period, such as 44A-163-B and 44B-163-W (Fig S7b). Therefore, the rate in which panicle increases in weight, prior and throughout grain filling appears to vary and may be important from a breeding perspective.

Surprisingly, the white commercial cultivar which was the first to lodge, was mostly stable in plot-height once lodged (around 35 cm above ground surface) during the entire grain filling and was the best yielding line. In the white commercial cultivar, despite stem weakness and the plant being bent towards the ground, the panicles are mostly above ground level. This pattern creates a medium level of lodging that appears to be different from the strong lodging where the plant is heavier and is totally bent to the ground (Fig S7b: 44B-163-W and 53-2-2-W).

Despite the large number of studies screening Teff lines (Assefa et al., 2003, Zeid et al., 2012, Girma et al., 2019, Nigus et al., 2016) there have been only few which include in-depth characterization of different lines. In addition, there are hardly any studies that present agronomic as well as sensory traits side by side to analyze possible links between them . The processing, eating, and nutritional quality of food products may be greatly influenced by Teff variety. Therefore, it is necessary to assess the genetic diversity of this crop for potential improvements of agronomic as well as edible traits. Newly breed varieties must be subjected to sensory analysis for consumer acceptance to make the research efforts commercially meaningful (Zhu, 2018). We report a significant genotypic effect on most of the sensory traits evaluated (Tables 9-10). The effectiveness of flour grinding was found to be crucial for texture across of all market samples. The white cultivars were ranked higher than the rest of the lines. The size of the grain may also effect Injera acidity and odor, as AGW was found to be positively correlated with odor intensity and negatively with acidity.

The current study growing conditions (pots and field experiments) were not favorable to observe the lodging resistance which was observed during original seed collection. The experiment didn't replicate the specific environmental context of a single seed developing in low density planted area and/or surrounded by a homogenous population of the plots which it was collected from. A wide genotypic variance was found in the current study for stem width and plant height. However, under an abundance of water and nutrient and, at high plant density, a thick stem does not ensure lodging resistance. It appears however that under low density and/or some sort of environmental stress may lead to increased stem lignification and hardening allowing the plant to carry the grain load at an erect posture. Future experimentation to test this hypothesis may include of combinations of agro-technics implementations such as: seed-coverage to enlarge seeds, using a mixture of Teff lines, reducing sowing density to reduce plant density, and the introduction of controlled stresses such as water deficiency and salinity. It is clear that late maturing, thick stem and tall Teff varieties possess deeper root systems than early maturing lines of shorter height (Ayele et al., 2001). Therefore, a combination that include lines that are characterized by thick stems with stress can improve lodging resistance. Integration between a wide range of parameters and the correlations obtained between agronomic and sensory traits may improve our ability to breed towards a "real world" better end-product.

Authors' contribution

LMO executed the experiments and wrote the manuscript. JB supervised agro-technics and sensory trial, NY executed sensory trial and helped with manuscript preparation. OAS and YK were involved in phenotyping and manuscript preparation. MR provided supervision, designed the experiments and wrote the manuscript.

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Tables and figure legends

Table 1.

List lines, average grain weight (AGW) of the initial seed set, seed color (W for white and B for brown). The phenotype of plant that grew in the greenhouse includes: AGW (mg), grain yield (gr/pot), stems per pot, grain per stem (gr), days from sawing to panicle emergence (DSP in days), maximal plant height (MPH in cm), and the proportion of brown out of white seeds, and out of total, quantified in grams.

Table 2.

Sensory evaluation questionnaire for the degree of consumer's acceptance satisfactions on to the Injera prepared from different lines and controls. The traits that were evaluated were: appearance (visual preference), color (color preference), odor (odor preference), odor intensity (odor strength), texture (softness), acidity (pungent) and flavor (taste preference). The judges were requested to taste the samples and indicate their response by rating their opinion on a five- point scale (1- "Strongly dislike"/lowest, and 5- "Like very much"/highest).

Table 3.

LS means for: TDM (Total Dry Matter, gr/plot), GY (Grain Yield, gr/plot), HI (Harvest Index), for the 11 lines under field conditions, as well as ANOVA for each of the traits.

Table 4.

LS means for: EGC (Early Ground Cover), LSD (Lower Stem width), USD (Upper stem width), for the 11 lines under field conditions, as well as ANOVA for each of the traits.

Table 5.

LS means for: Chla/gFW (Chlorophyll a), Chlb/gFW (Chlorophyll b), Chl/gFW (Total Chlorophyll), Chl a/b ratio, for the 11 lines under field conditions, as well as ANOVA for each of the traits.

Table 6.

LS means for: DSP (Days from Sowing to Panicle emergence), DPM (Days from Panicle emergence to Maturation), DSM (Days from Sowing to Maturation), for the 11 lines under field conditions, as well as ANOVA for each of the traits.

Table 7.

LS means for: AGW (Average Grain Weight), SL (Seed length), SpL (Spikelet length),

Table 8.

LS means for: MPH (Maximal Plot Height), DT<75% in 11 lines under field conditions, as well as ANOVA for each of the traits.

Table 9.

LS means for sensory traits: appearance (look preference), color (color preference), odor (odor preference), odor intensity (odor strength), for the 14 flour samples from the field experiment, as well as 3 market flours.

Table 10

LS means for sensory traits: texture (softness), acidity (strength) and flavor (taste preference). for the 11 lines flour samples from the field experiment, as well as 3 market control flours.

Table 11.

Coefficients of correlation (r) between TDM (Total Dry Matter), GY (Grain Yield), HI (Harvest Index), EGC (Early Ground Cover), LSD (Lower Stem width), USD (Upper stem width), Chla/gFW (Chlorophyll a), Chlb/gFW (Chlorophyll b), Chl/gFW (Total Chlorophyll), Chl a/b ratio, DSP (Days from Sowing to Panicle emergence), DPM (Days from Panicle emergence to Maturation), DSM (Days from Sowing to Maturation), AGW (Average Grain Weight), SL (Seed length), SpL (Spikelet length), MPH (Maximal Plot Height), DT<75% in 11 lines (Days to reach 75% of the plants lodging in a plot).

Figure 1.

Flow diagram of Injera preparation.

Figure 2.

Plot height (cm) averaged for each genotype as a function of days after sawing (DAS). The arrows indicate averaged date of panicle emergence under field condition.

Figure 3.

Images of the Spikelets of each of the 11 lines characterized in the field experiment.

Figure 4.

Images of Injera flat beard made from of each of the 11 lines characterized in the field experiment as well as three market controls.

Figure 5.

Principal component analysis (PCA) (based on correlation matrix) of continuous plant traits: TDM (Total Dry Matter),GY (Grain Yield), HI (Harvest Index), EGC (Early Ground Cover), LSD (Lower Stem width), USD (Upper stem width), Chla/gFW (Chlorophyll a), Chlb/gFW (Chlorophyll b), Chl/gFW (Total Chlorophyll), Chl a/b ratio, DSP (Days from Sowing to Panicle emergence), DPM (Days from Panicle emergence to Maturation), DSM (Days from Sowing to Maturation), AGW (Average Grain Weight), SL (Seed length), SpL (Spikelet length), MPH (Maximal Plot Height), DT<75%recorded on the 11 lines. Biplot vectors are trait factor loadings for PC1 and PC2.

Figure 6.

Color segregation in seeds and suggested genotypes.

Fig S1.

Two examples of Teff plants that didn't exhibit lodging in original plot locations. From these plants, and from other plants spotted, a single spike was collected for establishing the current seed collection.

Fig S2.

Genotype collection propagated in the greenhouse off season. Each genotype originated from a single spike was sawn in on pot.

Fig S3.

A field experimental plot design as well as an overview of the field at early (24 DAS) growth stages.

Supp. Fig 4.

Early growth cover evolution of plots in the field experiment. Images were analyzed using the *Coveragetool* (ref).

Supp. Fig 5.

Projected stem width of the first lowest node which bears one leaf ('Upper') and, b) the most basal internode ('Lower', below a), measured at 70 DAS.

Supp. Fig 6.

As a part of the process of average grain weight (AGW) evaluation, seeds were spread over a white sheet and photographed. For each plot the image was threshold using '*coveragetool*' (by sampling seeds to account) to be further processed by Image J's particle count tool.

Supp. Fig 7

A general overview of the ARO filed experiment which shows the wide phenotypic variance of the genetic material.

Supp. Fig 8

A survey on one of the: a) white cultivar, b) 44A-163-B, c) 44B-163-W, and d) 53-2-2-W plots at: 63,70,77,87 days after sawing at the ARO field experiment.

Table 1.

Line	**Seed color initial set**	**Brown/White**	**AGW initial set (mg)**	**Seed color seg**	**Brown/White**
White Teff	All white		0.23	all white	
44A-163-B	All brown		0.36	all brown	
44B-163-W	All white		0.27	all white	
53-1-M	53-1-W		0.60	53-1-W	
	53-1-B	0.021		53-1-B	0.064
53-2-M	White *		0.41	53-2-W	
				53-2-B	0.105
				53-2-1-W**	
				53-2-2-W**	
53-3-M	White *		0.48	53-3-W	
				53-3-B	0.015

* Undetectable light brown might exist

** Initiated from a single seed descent

Table 2.

Age:_____ Gender:_____	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Appearance (looks)														
Color														
Odor														
Odor intensity														
Texture														
Acidity														
Taste														
Remarks														

Table 3.

Trait	Line	LSM		Std. Error
TDM (kg/plot)	53-3-B	1.27	E	0.26
	White Teff	1.74	DE	0.10
	53-1-B	1.78	CDE	0.26
	44A-163-B	2.14	BC	0.13
	53-2-B	2.16	ABCD	0.26
	53-2-W	2.20	ABC	0.15
	44B-163-W	2.41	AB	0.13
	53-3-W	2.42	AB	0.13
	53-2-2-W	2.51	AB	0.18
	53-1-W	2.52	A	0.13
	53-2-1-W	2.54	AB	0.26
GY (kg/plot)	53-2-W	0.24	C	0.04
	53-3-W	0.25	C	0.03
	53-2-2-W	0.32	BC	0.04
	53-1-W	0.33	BC	0.03
	53-3-B	0.35	BC	0.06
	53-2-1-W	0.36	BC	0.06
	44B-163-W	0.39	B	0.03
	44A-163-B	0.41	B	0.03
	53-1-B	0.41	AB	0.06
	White Teff	0.50	A	0.03
	53-2-B	0.59	A	0.06
HI	53-3-W	0.10	E	0.01
	53-2-W	0.11	E	0.02
	53-2-2-W	0.13	DE	0.02
	53-1-W	0.13	DE	0.01
	53-2-1-W	0.14	CDE	0.03
	44B-163-W	0.16	CD	0.01
	44A-163-B	0.19	BC	0.01
	53-1-B	0.23	B	0.03
	53-2-B	0.27	A	0.03
	53-3-B	0.27	A	0.03
	White Teff	0.29	A	0.01
ANOVA	Source	DF	MS	Prob > F
Total DM	Model	10	0.340152	0.0008
	Error	20	0.065164	
	C. Total	30		
GY	Model	10	0.24667	<.0001
	Error	20	0.003783	
	C. Total	30		
HI	Model	10	0.014579	<.0001
	Error	20	0.000796	
	C. Total	30		

Table 4.

Trait	Line	LSM		Std. Error
EGC %	53-1-B	40.20	A	6.15
	53-2-B	37.40	AB	6.15

Trait	Line	LSM		Std. Error
	53-1-W	28.63	ABC	3.55
	53-2-1-W	23.60	ABCD	6.15
	44A-163-B	22.45	CD	3.08
	53-2-2-W	21.90	BCD	4.35
	44B-163-W	21.78	CD	3.08
	53-3-W	21.58	CD	3.08
	53-2-W	19.07	CD	3.55
	White Teff	15.22	D	2.75
	53-3-B	11.00	D	6.15
USD (cm)	53-3-W	0.33	A	0.02
	53-2-2-W	0.33	AB	0.03
	53-2-1-W	0.33	ABC	0.04
	53-1-W	0.30	ABC	0.02
	44B-163-W	0.29	BC	0.02
	53-2-B	0.27	BCD	0.04
	53-2-W	0.26	CD	0.02
	53-3-B	0.25	BCD	0.04
	44A-163-B	0.25	CD	0.02
	53-1-B	0.24	BCD	0.04
	White Teff	0.22	D	0.02
LSD (cm)	53-2-2-W	0.31	A	0.02
	53-3-W	0.24	B	0.01
	53-2-1-W	0.24	ABC	0.03
	53-1-W	0.22	BC	0.01
	44B-163-W	0.22	BC	0.01
	53-2-W	0.21	BCD	0.02
	44A-163-B	0.20	CD	0.01
	53-1-B	0.19	BCD	0.03
	53-3-B	0.18	BCD	0.03
	White Teff	0.18	D	0.01
	53-2-B	0.15	D	0.03
ANOVA	Source	DF	MS	Prob > F
EGC	Model	10	108.137	0.0253
	Error	18	37.827	
	C. Total	28		
USD	Model	10	0.004629	0.0118
	Error	20	0.001421	
	C. Total	30		
LSD	Model	10	0.003712	0.0015
	Error	20	0.000785	
	C. Total	30		

Table 5.

Trait	Line	LSM		Std. Error
Chla/gFW	53-3-B	226.88	A	36.27
	44B-163-W	165.05	AB	18.14
	53-2-1-W	164.64	AB	36.27
	53-1-B	162.59	AB	36.27

Trait	Line	LSM		Std. Error
	53-1-W	143.60	AB	18.14
	White Teff	136.22	B	14.81
	44A-163-B	136.01	B	18.14
	53-3-W	122.68	B	18.14
	53-2-2-W	120.36	B	25.65
	53-2-W	118.18	B	20.94
	53-2-B	107.90	B	36.27
Chlb/gFW	53-3-B	145.36	A	17.41
	53-1-B	105.44	A	17.41
	44B-163-W	56.88	B	17.41
	White Teff	49.25	B	17.41
	53-1-W	48.80	B	12.31
	53-2-1-W	47.67	B	10.05
	44A-163-B	46.01	B	8.71
	53-2-B	39.49	B	8.71
	53-2-2-W	38.38	B	8.71
	53-3-W	34.86	B	8.71
	53-2-W	32.61	B	7.11
Chl/gFW	53-3-B	372.12	A	48.76
	53-1-B	267.95	AB	48.76
	44B-163-W	221.87	B	24.38
	53-2-1-W	212.26	B	48.76
	53-1-W	192.35	B	24.38
	White Teff	185.42	B	19.91
	44A-163-B	181.97	B	24.38
	53-2-2-W	158.71	B	34.48
	53-3-W	157.50	B	24.38
	53-2-W	150.75	B	28.15
	53-2-B	147.35	B	48.76
a/b ratio	53-2-W	3.60	A	0.49
	53-3-W	3.50	AB	0.43
	53-2-1-W	3.45	AB	0.85
	44A-163-B	3.41	AB	0.43
	44B-163-W	3.17	AB	0.43
	53-2-2-W	3.14	AB	0.60
	White Teff	2.97	AB	0.35
	53-1-W	2.91	AB	0.43
	53-2-B	2.73	AB	0.85
	53-3-B	1.56	AB	0.85
	53-1-B	1.54	B	0.85
ANOVA	Source	DF	MS	Prob > F
Chla/gFW	Model	10	1580.63	0.3469
	Error	20	1315.62	
	C. Total	30		
Chlb/gFW	Model	10	1463.88	0.0014
	Error	20	303.14	
	C. Total	30		
Chl/gFW	Model	10	5683.21	0.0466
	Error	20	2377.74	
	C. Total	30		

Trait	Line	LSM		Std. Error
a/b ratio	Model	10	0.71	0.4878
	Error	20	0.72	
	C. Total	30		

Table 6.

Trait	Line	LSM		Std. Error
DSP	53-3-W	64.00	A	0.70
	53-2-2-W	63.00	AB	0.99
	53-1-W	62.25	AB	0.70
	44B-163-W	62.25	AB	0.70
	53-2-W	62.00	ABC	0.81
	53-2-1-W	60.00	BCD	1.40
	44A-163-B	60.00	C	0.70
	53-2-B	56.00	DE	1.40
	53-3-B	56.00	DE	1.40
	White Teff	53.50	E	0.57
	53-1-B	53.00	E	1.40
DPM	53-3-W	46.00	A	2.32
	53-1-B	43.00	AB	4.64
	53-2-B	40.00	ABC	4.64
	53-3-B	40.00	ABC	4.64
	53-2-2-W	37.00	BC	3.28
	53-2-1-W	36.00	ABC	4.64
	53-2-W	36.00	BC	2.68
	White Teff	35.83	BC	1.89
	53-1-W	35.25	BC	2.32
	44B-163-W	34.25	BC	2.32
	44A-163-B	31.00	C	2.32
DSM	53-3-W	110.00	A	2.35
	53-2-2-W	100.00	B	3.33
	53-2-W	98.00	BC	2.72
	53-1-W	97.50	BC	2.35
	44B-163-W	96.50	BC	2.35
	53-1-B	96.00	BCD	4.71
	53-2-1-W	96.00	BCD	4.71
	53-2-B	96.00	BCD	4.71
	53-3-B	96.00	BCD	4.71
	44A-163-B	91.00	CD	2.35
	White Teff	89.33	D	1.92
ANOVA	Source	DF	MS	Prob > F
DSH	Model	10	46.6935	<.0001
	Error	20	1.95	
	C. Total	30		
DHM	Model	10	57.586	0.03
	Error	20	21.5167	
	C. Total	30		
DSM	Model	10	119.4215	0.0007
	Error	20	22.1667	

Trait	Line	LSM	Std. Error
	C. Total	30	

Table 7.

Trait	Line	LSM		Std. Error
AGW (gr)	53-1-B	0.51	A	0.0005
	44B-163-W	0.49	A	0.0005
	53-3-B	0.48	AB	0.0005
	53-2-W	0.47	A	0.0005
	White Teff	0.42	A	0.0004
	53-2-B	0.38	ABC	0.0004
	53-3-W	0.34	BC	0.0003
	44A-163-B	0.32	C	0.0003
	53-2-2-W	0.32	C	0.0003
	53-1-W	0.30	C	0.0003
	53-2-1-W	0.25	C	0.0002
Σεεδ λενγτη (μμ)	53-1-B	1341	A	53
	53-3-B	1340	A	53
	53-2-2-W	1251	AB	37
	53-2-B	1243	ABC	53
	53-1-W	1215	B	26
	44A-163-B	1188	BC	26
	White Teff	1176	BC	21
	53-2-W	1171	BC	30
	53-2-1-W	1161	BCD	53
	44B-163-W	1129	CD	26
	53-3-W	1054	D	26
Σπικελετ λενγτη (μμ)	44B-163-W	7986	A	440
	53-2-B	7051	AB	440
	White Teff	6855	AB	341
	53-2-1	6819	B	288
	44A-163-B	6714	B	341
	52-2-W	6700	B	440
	53-1-W	6613	B	341
	53-3-B	6291	B	440
	53-2-2-W	5933	BC	440
	53-1-B	5882	BC	440
	53-3-W	4945	C	381
ANOVA	Source	DF	Mean Square	Prob > F
AGW	Model	10	1.84E-08	0.00147
	Error	20	3.86E-09	
	C. Total	30		
Seed length	Model	10	14513	0.00081
	Error	20	2765	
	C. Total	30		.
Spikelet length	Model	10	2111806	0.00238
	Error	33	580102	
	C. Total	43		

Table 8.

DAS		LSM		Std. Error	DAS		LSM		Std. Error
53	53-2-B	55.00	A	4.42	**63**	53-3-B	70.33	A	7.72
	White Teff	50.67	A	1.80		53-2-1-W	68.40	A	7.72
	44A-163-B	50.50	AB	2.21		53-2-2-W	65.51	A	5.46
	53-2-1-W	50.00	ABC	4.42		44A-163-B	64.58	A	3.86
	53-1-B	50.00	ABC	4.42		53-3-W	62.97	A	3.86
	53-2-2-W	48.50	ABC	3.12		53-1-W	60.34	A	3.86
	53-1-W	46.25	ABC	2.21		53-2-W	60.31	A	4.46
	53-2-W	44.00	BC	2.55		44A-163-B	53.27	AB	3.86
	53-3-W	40.75	C	2.21		53-2-B	49.00	BC	7.72
	53-3-B	38.00	CD	4.42		53-1-B	36.20	BC	7.72
	44B-163-W	34.00	D	2.21		White Teff	32.98	C	3.15
56	White Teff	63.06	A	1.66	**67**	53-3-B	76.00	AB	9.42
	44A-163-B	62.83	A	2.04		53-3-W	73.67	A	4.71
	53-1-B	60.33	AB	4.07		44B-163-W	73.09	A	4.71
	53-2-B	58.00	AB	4.07		53-2-W	71.69	AB	5.44
	53-2-2-W	57.17	AB	2.88		44A-163-B	67.95	AB	4.71
	53-2-1-W	56.00	BC	4.07		53-2-2-W	66.59	AB	6.66
	53-1-W	54.50	B	2.04		53-2-1-W	64.60	AB	9.42
	53-2-W	53.22	BC	2.35		53-1-W	57.54	B	4.71
	53-3-W	47.08	CD	2.04		53-2-B	54.08	ABC	9.42
	53-3-B	45.00	CD	4.07		White Teff	35.84	CD	3.84
	44B-163-W	41.58	D	2.04		53-1-B	25.85	D	9.42
60	53-2-1-W	70.00	AB	7.37	**70**	53-3-B	78.00	A	12.90
	53-2-2-W	69.00	A	5.21		53-2-W	66.17	A	7.45
	44A-163-B	64.00	AB	3.68		44B-163-W	65.00	A	6.45
	53-2-W	62.33	AB	4.25		53-3-W	63.83	A	6.45
	53-3-B	60.00	AB	7.37		44A-163-B	59.56	A	6.45
	53-1-W	59.75	AB	3.68		53-2-2-W	52.41	AB	9.12
	53-3-W	59.50	AB	3.68		53-1-W	51.47	AB	6.45
	44B-163-W	56.25	AB	3.68		53-2-B	46.50	BC	12.90
	53-2-B	56.00	AB	7.37		53-2-1-W	45.80	BC	12.90
	53-1-B	49.00	BC	7.37		White Teff	30.43	C	5.27
	White Teff	36.00	C	3.01		53-1-B	24.75	BC	12.90
75	53-2-W	69.00	A	8.01	**77**	53-3-W	59.98	A	8.10
	53-3-W	67.27	A	6.94		53-2-W	59.78	A	9.35
	53-3-B	61.80	AB	13.88		44A-163-B	52.01	A	8.10
	44A-163-B	53.51	AB	6.94		53-2-2-W	48.42	AB	11.46
	53-2-B	52.50	ABC	13.88		53-2-B	46.67	AB	16.20
	53-2-2-W	47.92	ABC	9.81		53-1-W	39.71	AB	8.10
	53-1-W	45.43	BC	6.94		53-3-B	35.17	AB	16.20
	44B-163-W	36.60	BC	6.94		53-2-1-W	32.60	AB	16.20
	53-2-1-W	31.65	BC	13.88		White Teff	28.04	B	6.61
	53-1-B	30.17	BC	13.88		44B-163-W	26.94	B	8.10
	White Teff	27.48	C	5.67		53-1-B	23.50	AB	16.20
MPH (cm)	53-3-B	78.00	AB	6.08	**DT <75%**	53-3-B	77.00	A	4.39
	53-2-W	76.45	A	3.51		44B-163-W	75.50	A	2.19
	44B-163-W	75.34	A	3.04		53-2-W	72.33	AB	2.53
	53-3-W	71.03	ABC	3.51		53-3-W	72.33	AB	2.53

DAS		LSM		Std. Error	DAS		LSM		Std. Error
	44A-163-B	69.66	ABCD	3.04		53-2-1-W	67.00	ABC	4.39
	53-2-2-W	66.59	ABCD	4.30		53-1-W	65.50	BC	2.19
	53-1-W	65.75	BCD	3.04		53-2-2-W	65.00	BC	3.10
	53-2-1-W	64.60	ABCD	6.08		53-1-B	63.00	BC	4.39
	White Teff	61.59	D	2.48		44A-163-B	61.50	C	2.19
	53-1-B	60.33	BCD	6.08		White Teff	60.00	C	4.39
	53-2-B	58.00	CD	6.08		53-2-B	60.00	C	1.96

ANOVA				
	Source	DF	MS	Prob > F
53	Model	10	109.33	5E-04
	Error	20	19.52	
	C. Total	30		
56	Model	10	176.10	<.0001
	Error	20	16.58	
	C. Total	30		
60	Model	10	348.07	2E-04
	Error	20	54.26	
	C. Total	30		
63	Model	10	476.46	<.0001
	Error	20	59.66	
	C. Total	30		
67	Model	10	718.17	<.0001
	Error	20	88.68	
	C. Total	30		
70	Model	10	632.19	0.005
	Error	20	166.43	
	C. Total	30		
75	Model	10	676.29	0.01
	Error	20	192.63	
	C. Total	30		
77	Model	10	532.08	0.086
	Error	20	262.48	
	C. Total	30		
MPH (cm)	Model	10	155.339	0.004
	Error	20	38.012	
	C. Total	30		
DT <75%	Model	10		
	Error	20		
	C. Total	30		

Table 9.

Trait	Line	LSM		Std. Error
appearance	44B-163-W	4.38	A	0.32
	53-3-B	4.13	A	0.30
	White Market I	4.08	AB	0.32

Trait	Line	LSM		Std. Error
	53-2-W	4.00	AB	0.32
	53-2-2-W	3.92	AB	0.32
	Brown Market I	3.92	AB	0.32
	White Market II	3.69	ABC	0.32
	White Teff	3.57	ABC	0.31
	53-3-W	3.23	BCD	0.32
	44A-163-B	3.00	CDE	0.32
	53-1-W	2.92	CDE	0.32
	53-2-B	2.54	DE	0.32
	53-1-B	2.15	EF	0.32
	53-2-1-W	1.58	F	0.34
Color	53-3-B	4.47	A	0.28
	44B-163-W	4.15	AB	0.30
	53-2-2-W	4.08	ABC	0.30
	53-2-W	4.08	ABC	0.30
	White Market I	4.08	ABC	0.30
	Brown Market I	3.85	ABCD	0.30
	White Teff	3.77	ABCD	0.30
	53-1-W	3.62	BCD	0.30
	White Market II	3.62	BCD	0.30
	53-1-B	3.31	CDE	0.30
	53-3-W	3.31	CDE	0.30
	44A-163-B	3.23	DE	0.30
	53-2-B	2.54	EF	0.30
	53-2-1-W	1.75	DF	0.31
Odor	44B-163-W	3.77	A	0.39
	53-3-B	3.73	A	0.36
	44A-163-B	3.69	AB	0.39
	Brown Market I	3.23	ABC	0.39
	53-1-W	3.00	ABCD	0.39
	White Market I	2.92	ABCD	0.39
	White Market II	2.92	ABCD	0.39
	53-1-B	2.85	ABCDE	0.39
	53-2-2-W	2.77	ABCDE	0.39
	White Teff	2.71	ABCDE	0.38
	53-2-W	2.62	BCDE	0.39
	53-2-B	2.23	CDE	0.39
	53-3-W	2.08	DE	0.39
	53-2-1-W	1.75	EF	0.41
Odor intensity	53-2-1-W	3.92	A	3.92
	53-3-W	3.23	AB	3.23
	White Market II	3.23	AB	3.23
	53-2-W	3.08	ABC	3.08
	53-2-2-W	2.92	ABC	2.92
	53-2-B	2.85	ABC	2.85
	53-1-W	2.77	BC	2.77
	White Teff	2.71	BC	2.71
	53-1-B	2.62	BC	2.62
	White Market I	2.54	BC	2.54
	44B-163-W	2.46	BC	2.46

Trait	Line	LSM		Std. Error
	53-3-B	2.40	BC	2.40
	Brown Market I	2.38	BC	2.38
	44A-163-B	2.08	C	2.08
ANOVA	Source	DF	MS	Prob > F
appearance	Model	13	8.83	<.0001
	Error	170	1.37	
	C. Total	183		
Color	Model	13	6.53	<.0001
	Error	169	1.18	
	C. Total	182		
Odor	Model	13	4.79	0.01
	Error	170	1.97	
	C. Total	183		
Odor intensity	Model	13	2.72	0.21
	Error	170	2.07	
	C. Total	183		

Table 10.

Trait	Line	LSM		Std. Error
Texture	Brown Market I	3.92	A	0.36
	White Market I	3.92	A	0.36
	44A-163-B	3.85	A	0.36
	White Teff	3.71	A	0.34
	53-3-B	3.64	AB	0.34
	White Market II	3.62	AB	0.36
	53-2-2-W	3.54	ABC	0.36
	53-2-W	3.46	ABC	0.36
	53-2-B	3.08	ABCD	0.36
	53-1-B	3.00	ABCD	0.36
	53-2-1-W	2.67	BCDE	0.37
	44B-163-W	2.62	CDE	0.36
	53-1-W	2.46	DE	0.36
	53-3-W	2.00	E	0.36
Acidity	53-2-2-W	3.38	A	0.40
	53-1-W	3.08	AB	0.40
	44A-163-B	3.08	AB	0.40
	White Teff	2.93	ABC	0.38
	53-1-B	2.85	ABC	0.40
	53-2-W	2.85	ABC	0.40
	53-3-W	2.54	ABCD	0.40
	44B-163-W	2.46	ABCD	0.40
	53-2-B	2.46	ABCD	0.40
	53-3-B	2.14	BCDE	0.38
	White Market I	2.00	BCDE	0.40
	White Market II	2.00	BCDE	0.40
	53-2-1-W	1.91	CD	0.43
	Brown Market I	1.69	DE	0.40
Flavor	53-3-B	3.50	A	0.33

Trait	Line	LSM		Std. Error
	44A-163-B	3.23	AB	0.35
	Brown Market I	3.15	ABC	0.35
	44B-163-W	3.08	ABC	0.35
	53-1-B	3.00	ABC	0.35
	White Market II	2.92	ABCD	0.35
	White Teff	2.79	ABCD	0.33
	White Market I	2.69	ABCD	0.35
	53-2-W	2.38	BCDE	0.35
	53-2-2-W	2.31	BCDEF	0.35
	53-1-W	2.23	CDEF	0.35
	53-3-W	2.00	DEF	0.35
	53-2-B	1.69	EF	0.35
	53-2-1-W	1.36	F	0.38
ANOVA	Source	DF	MS	Prob > F
Texture	Model	13	4.91	0.0006
	Error	169	1.65	
	C. Total	182		
Acidity	Model	13	3.46	0.0717
	Error	168	2.07	
	C. Total	181		
Flavor	Model	13	4.86	0.0004
	Error	168	1.56	
	C. Total	181		

Table 11.

	TDM	GY	HI	EGC	USD	LSD	Chla	Chlb	Chl.	DSP	DPM	DSM	a/b ratio
TDM													
GY	-0.29												
HI	-0.79	0.81											
EGC	0.24	0.39	0.06										
USD	0.79	-0.48	-0.75	0.03									
LSD	0.63	-0.63	-0.74	-0.20	0.77								
Chla	-0.59	-0.09	0.32	-0.35	-0.20	-0.19							
Chlb	**-0.80**	0.05	0.53	-0.11	-0.42	-0.35	0.88						
Chl.	-0.72	-0.02	0.44	-0.23	-0.32	-0.28	0.97	0.97					
DSP	0.78	-0.69	-0.91	-0.23	0.77	0.71	-0.31	-0.56	-0.45				
DPM	-0.21	-0.12	0.05	0.27	0.15	-0.07	0.04	0.28	0.17	-0.17			
DSM	0.41	-0.62	-0.64	0.05	0.70	0.48	-0.21	-0.19	-0.21	0.61	0.67		
a/b ratio	0.29	-0.32	-0.37	0.46	0.52	0.31	0.08	0.14	0.11	0.20	0.44	0.50	
AGW	-0.64	0.09	0.41	-0.03	-0.64	-0.46	0.35	0.54	0.46	-0.45	0.22	-0.16	-0.04
SL	-0.62	0.29	0.57	0.26	-0.44	-0.28	0.46	0.73	0.62	-0.63	0.10	-0.39	0.30
SpL	0.07	0.46	0.24	-0.03	-0.26	-0.32	0.10	-0.10	0.00	-0.10	-0.71	-0.65	-0.24
MPH	0.66	-0.81	-0.92	-0.21	0.68	0.74	-0.23	-0.46	-0.36	0.79	-0.12	0.50	0.28
DT <75%	-0.07	-0.64	-0.36	-0.52	0.26	0.19	0.52	0.34	0.44	0.43	0.18	0.47	0.24
appear.	-0.20	-0.29	-0.05	-0.65	-0.14	0.15	0.11	0.08	0.10	0.28	-0.17	0.07	-0.28
Color	-0.37	-0.33	0.03	-0.50	-0.29	0.10	0.25	0.32	0.29	0.10	-0.07	0.03	-0.16
Odor	-0.40	0.02	0.25	-0.30	-0.44	-0.16	0.49	0.48	0.50	-0.06	-0.43	-0.39	-0.37
Odor int.	0.49	-0.28	-0.46	0.06	0.63	0.37	-0.22	-0.39	-0.31	0.27	0.27	0.42	0.49

	TDM	GY	HI	EGC	USD	LSD	Chla	Chlb	Chl.	DSP	DPM	DSM	a/b ratio
Text.	-0.55	0.28	0.52	-0.33	-0.64	-0.20	0.09	0.22	0.16	-0.43	-0.46	-0.69	-0.49
Acid.	0.18	-0.08	-0.16	0.12	-0.13	0.32	-0.53	-0.34	-0.45	0.15	-0.26	-0.09	-0.19
Flav.	-0.66	0.01	0.40	-0.33	-0.64	-0.26	0.53	0.62	0.60	-0.31	-0.19	-0.39	-0.45

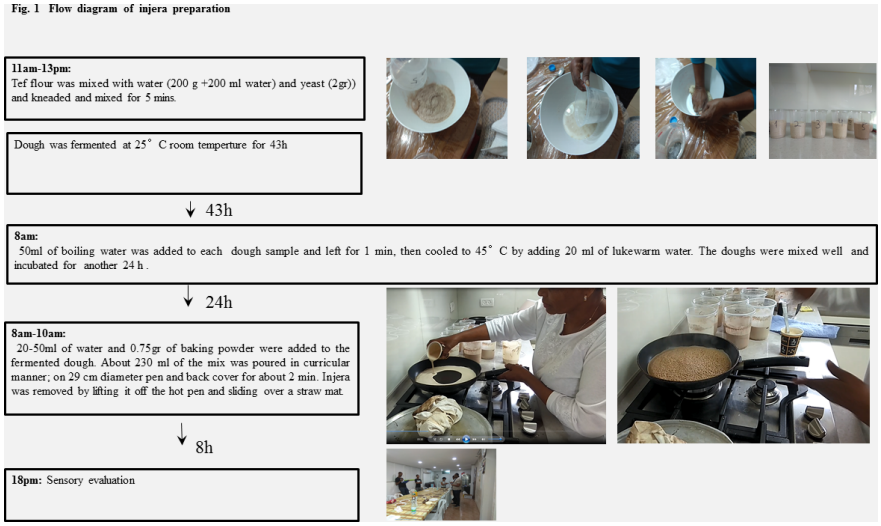

Fig. 2

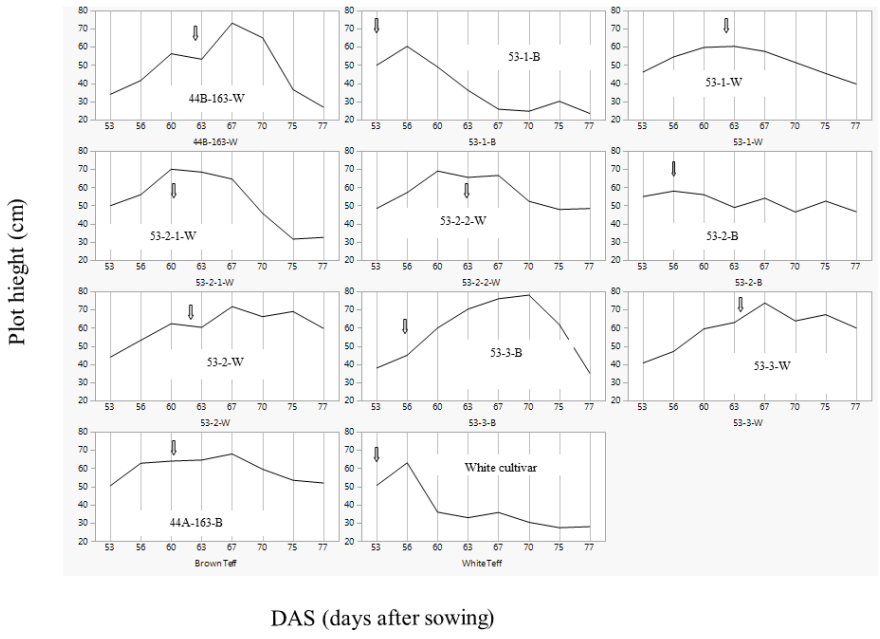

Fig. 3

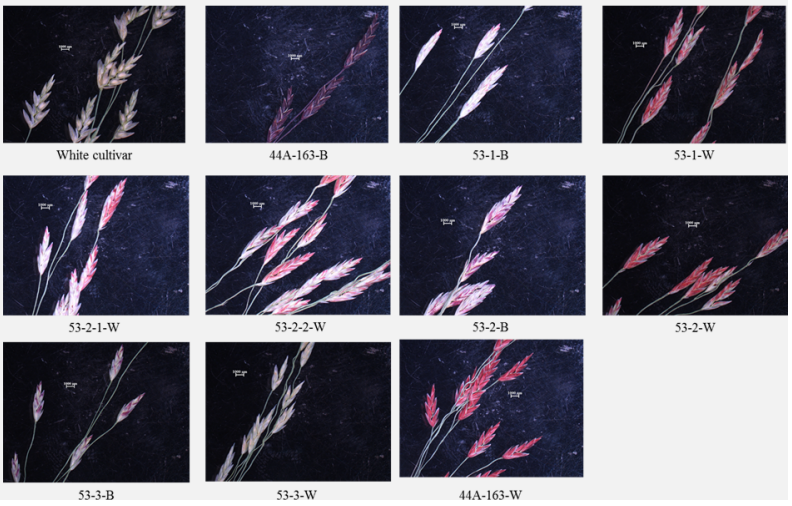

Fig. 4

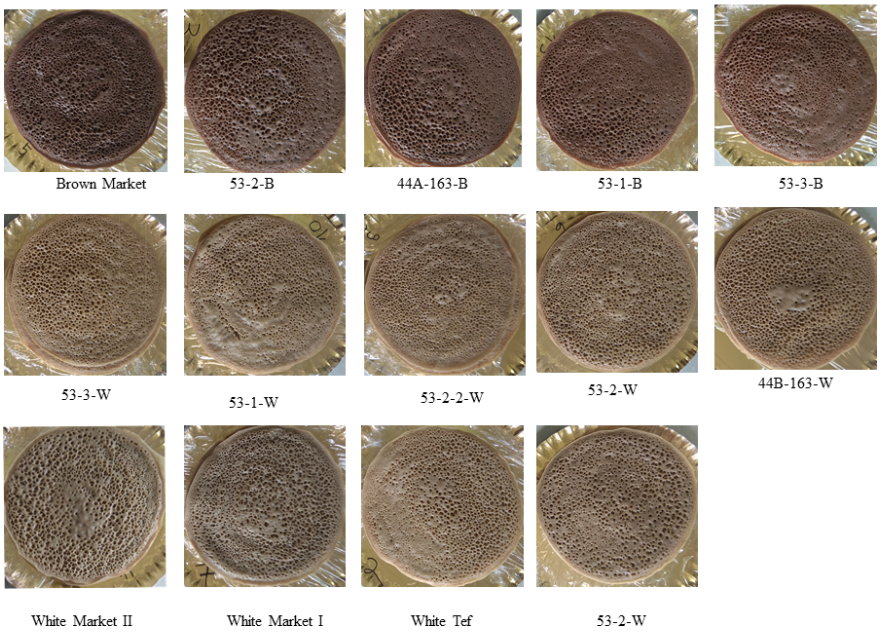

Fig. 5

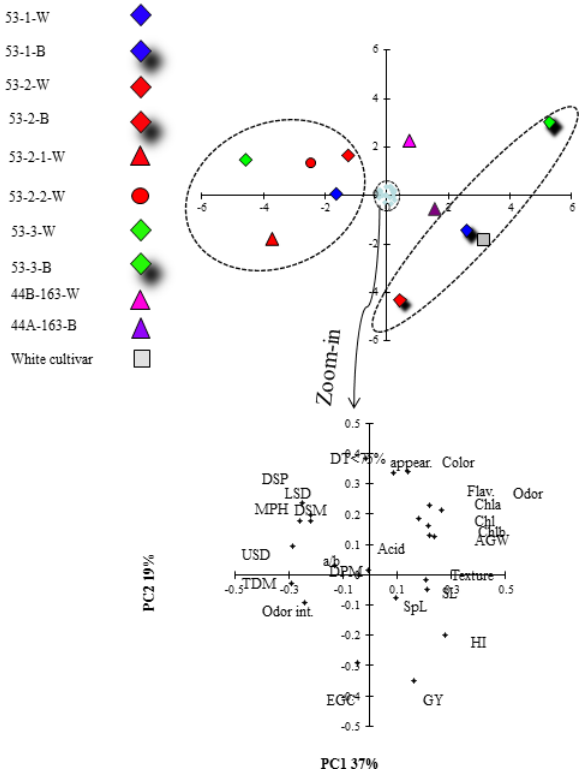

Fig. 6

53-1 mixed color seed from greenhouse after propagation
white: aabb (0.937)
brown: Aabb/aaBb/AaBb (0.0625)

53-1-B, 53-2-B and 53-3-B (left to right), mostly brown, harvested from ARO field experiment
white: aabb
brown: Aabb/aaBb/AaBb/AABB/AbBB/AABb