



Developmental plasticity: a phenological mechanism to endure later stage water deficit stresses in tef [*Eragrostis tef* (Zucc.) Trotter] varieties

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ABSTRACT

Water deficit at later growth stages (terminal drought) is a major abiotic factor limiting productivity of crops in northern Ethiopia. Varietal selection is among sustainable solutions to curb the problem. In line with this, a study was conducted in Tigray region, northern Ethiopia during 2011 and 2012 main cropping seasons to investigate the phenotypic diversity in tef varieties for developmental plasticity under severe water stress. Fifteen tef varieties were tested under late season water stress. Deferred/delay sowing time by two weeks was applied to expose the varieties to water stress. Soil and crop data were collected and analyzed. The varieties have shown significant ($p < 0.001$) interaction with the imposed stresses both for days to maturity and panicle length. Varieties such as DZ-01-974, DZ-01-899, DZ-cr-358 and *Berkayi* tend to tolerate the effect of terminal drought by shortening their maturity time, which is referred as drought escape. In contrast, varieties like DZ-01-99, DZ-01-358 and *AbatNech* have significantly reduced in length of their panicle. This is the actively transpiring part during later growth stage, without significant yield loss. This phenotyping for developmental plasticity has indicated that the tef employ escaping and reduction of evaporative surfaces to overcome the severe effects of terminal drought. To tailor varieties that better suit for drought prone farming systems. Such drought-adaptive traits should be targeted in breeding programs.

Keywords: Tef; Delayed planting; Maturity; Panicle; Drought escape and avoidance; Ethiopia.

1. INTRODUCTION

Tef (*Eragrostis tef*) is dominantly grown in Ethiopia as a staple food crop. It covers about 22.95% of the arable land under cereal crops production (CSA, 2016) with annual average national productivity of not more than 1.2t ha⁻¹. Despite the low national average yield, the crop has good genetic potential to yield even up to 6t ha⁻¹ under different sound soil – water – crop management practices (Tareke et al., 2013). Tef is predominantly grown in arid and semi-arid parts of Ethiopia and as a result perceived as terminal drought tolerant crop (Cottum, 2014; Kebebew et al., 2011). Water stress imposed during various different growth stages of tef inflicts very different scale of impacts on the crop (Mengistu, 2009; Yenesew et al., 2013). The reproductive stages of tef is, however, marked as the most susceptible to water stress and this stage coincides with the most recurrent terminal drought of Ethiopia.

Water stress adversely impacts many aspects of the physiological processes of plants and if the stress is prolonged, plant growth, and productivity are severely diminished. Plants have evolved complex physiological and biochemical adaptations to adjust and adapt to a variety of environmental stresses (Osakabe et al., 2014). Drought escape which is defined as the ability of the crop to complete its life cycle before serious soil and crop water deficits develop. The escape mechanism involves rapid phenological development (early flowering and early maturity), developmental plasticity (variation in duration of growth period depending on the extent of water deficit), and remobilization of assimilates to the grain (Beebe et al., 2013). Developmental plasticity (DP) is studied as an important response mechanism in various crops to adapt to the adverse effects of environmental stresses (Ha et al., 2014; Nishiyama et al., 2013). For instance, initiation of fairly high number of secondary tillers after the death of primary tillers due to mid-season drought and early maturity are the mechanisms employed by pearl millers to adapt drought (Vadez et al., 2012). Nevertheless, DP is not the mechanism employed by all crop species rather featured in some crop species. Some crops effectively tolerate drought through mobilization and utilization of sink organ reserves for grain filling under drought stress conditions (Blum, 2005). This in fact limits the growth of sink organs such as growth in height, branches and heads. Understanding of the effect of drought stress on growth and development of crops is hence important to improve crops stress tolerance in crop improvement programs. Very many shoot and root related traits are reported to contribute to the drought tolerance of crops (Beebe et al., 2013). Sustaining tillers to contribute to final yield (Vadez et al., 2012) and shortening the time taken between floral initiation and maturity (Muñoz-Perea et al., 2007; Foster et al., 1995) are among the traits known to contribute to drought tolerance. The expression of traits contributing to drought tolerance has to be evaluated in the specific field environments in which the crop is to be grown to generate precise information (Condon et al., 2004). These traits can, indeed, help to discriminate among different crop varieties. For tef, the contribution of shoot related traits to its drought tolerance and diversity of tef genotypes for these traits was not studied though it is frequently exposed to terminal drought. Therefore, the aim of this study were to i) investigate whether or not tef adapt the adverse effect of terminal drought through developmental plasticity and ii) analyze the phenotypic diversity among 15 tef varieties for developmental plasticity traits under water stress conditions.

2. MATERIALS AND METHODS

2.1. Experimental Site and its Climate

Field experiment was conducted at Mekelle University research station in Tigray region, Ethiopia during the main cropping seasons of 2011/12 and 2012/13 to evaluate the performances of tef varieties under terminal drought. Geographically, the site is located at 13⁰28'N latitude, 39⁰29'E longitude and altitude of 2212 meter above sea level in the northern Ethiopia. Tigray is among the semi-arid regions and characterized by erratic rainfall, frequent drought and a harsh cropping environment. In most cases, the rain commences in the last week of June and ends in the second week of September which implies that the area receive rain for less than 3 months. The mean seasonal (June; July; August and September) rainfall of the area is 450mm (Araya and Stroosnijder, 2010) where July and August contribute more than 80% of the amount. Its average seasonal temperature is 18.5⁰C with maximum and minimum of 26⁰C and 12.5⁰C, respectively. The analysis of sampled soil of the site confirms that the soil is clay loam with 28.7 and 17.8 volume percent, averaged over soil depth of 0- 40cm, water content at field capacity and permanent wilting points, respectively as measured by gravimetric method. Unless the rainfall continues to at least the third week of September, crops are exposed to water stress during their reproductive stages.

2.2. Experimental Design and Treatments

A split plot design was used to accommodate the three factors viz. year, water levels and varieties. The year factor was assigned to the main plot while water level and varieties were assigned to the sub-plot and sub-sub-plots, respectively. To coincide the reproductive (booting to grain filling) stages with water stress, delayed sowing approach was employed. The sowing time was deliberately delayed by 15 days beyond the customized tef sowing calendar of the area. Sowing was performed on 3rd of August in 2011 and 2nd of August in 2012 at a seeding rate of 15kg ha⁻¹ for each variety on 3m² plot.

In both years, fifteen tef varieties (10 improved and 5 local: lists are given in Table 1) were tested under a diverse set of water conditions that ranged from favorable irrigated (2I, non-stress) to moderate (1I) and severe stresses (no irrigation, RF) during their reproductive – stages. These water conditions were create after the rain stopped, which coincided with booting stages of most of the tested varieties. All agronomic practices, except watering, recommended for tef were applied equally for all the fifteen varieties.

Table 1. List and description of tef varieties included in the study.

<i>Variety</i>	<i>Status</i>	<i>Release year</i>	<i>Description</i>
1. DZ-01-974	Improved	1995	Pale white seeded variety which takes about 3 ½ months to mature. In conducive environments, it is high yielding.
2. DZ-cr-37	Improved	1984	White seeded variety developed for moisture stress areas
3. DZ-cr-387	Improved	2006	Very white seeded, relatively late maturing with higher yielding potential
4. DZ-01-99	Improved	1970	Brown seeded with wide range of maturity date and yield gap
5. DZ-01-1285	Improved	2002	White seeded, takes upto 4 months to mature with yielding potential of upto 2.5t ha ⁻¹
6. DZ-01-899	Improved	2005	Pale white seeded, late maturing dwarf variety
7. DZ-cr-358	Improved	1995	Grown in various ecology with wide range (76-138) maturity days, shows wider yield gap (0.3-1.2t ha ⁻¹)
8. DZ-01-1281	Improved	2002	Early maturing white seeded variety with wider yield gap
9. DZ-01-1681	Improved	2002	Dark brown seed color, early maturing, wider yield gap
10. DZ-01-196	Improved	1978	Attractive white color seeded, early maturing but less yielder.
11. Abat Key	Local	-	# Red colored cultivated in moisture stress areas
12. AbatNech	Local	-	#White colored cultivated in moisture stress areas
13. Berkayi	Local	-	#White and large seeded variety grown in western Tigray
14. Kobo	Local	-	#White and large seeded variety grown in western Tigray
15. Wofey	Local	-	Mixed color (white and red)

(Sources: Kebebew et al., 2011; # farmers' description).

The soil moisture content of each lock was monitored before each irrigation, starting from the first irrigation, every five days using Time Domain Reflectometry (TDR) probe. Both irrigations, 1I and 2I, were applied after the soil moisture content was dropped below the field capacity of the soil. The probe measures volumetric soil moisture content expressed in m³/m³. PVC pipes were installed to a depth of 1 meter in each plot to provide access for inserting the TDR probe into the soil. Moisture measurement was done at five days interval before the next irrigation in all plots of the treatment. Soil moisture measurements were carried out at depth intervals of 0-20, 21- 40 and 41- 60 cm (Fig 1). The measurements taken at this depths were used to represent the root coverage of the different tef varieties.

2.3. Plant Data Collection

The focus of this study is to investigate the shoot related traits to phenotype tef varieties for terminal drought tolerance. Panicle length from morphological traits and days to maturity from phenological traits were collected and analyzed. Shoot traits are associated with plant growth and development, and are constitutive rather than stress-induced (Chaves et al., 2003).

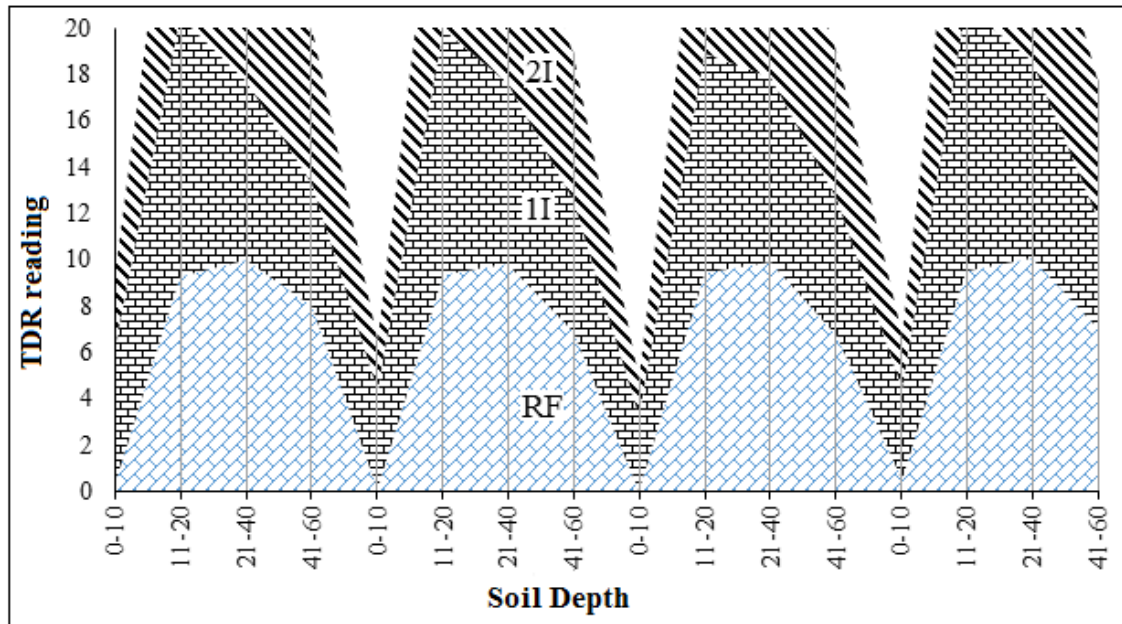


Figure 1. Sketch of TDR measured soil water content at different soil depth of the three tef growing conditions (Note: RF: Severe stress; 1I: Moderate stress; 2I: Non-stress).

2.4. Data Analysis and Interpretation

Acquired data were exposed to rigorous statistical analysis for variance partitioning and mean comparison using Genstat-14.1 statistical software. Since the focus of the study was to understand the performance of the varieties under the three water regime, a model structure “*year+ supplementary irrigation*variety*” was used during the analysis. This model is in fact helped to remove the complexity of three way interaction by reducing the interaction effect to the actual split plot design used in the field. The mean performance of the traits due to the three factors main effects and an interaction effect from supplementary irrigation \times varieties were compared using least significance difference (LSD) test at alpha level of 1% and 5% for highly significant and significant effects, respectively.

3. RESULTS

3.1. Soil Water Content

The root zone water depletion was assumed close to the permanent wilting point (PWP) as early senescence was noticed. Figure 1 shows soil moisture contents from the TDR reading from the three treated plots. Always, the soil moisture content in all intervals of the soil depth from non-irrigate (RF) plots is very much lower than its value for the moderately stressed and non-stressed plots. Moisture content in the top 10cm depth rooting zone is very minimal to support the crop water need. Under stress conditions the suction forces from the soil particle to the water molecule held in the micro pore should stronger than the force applied from the crop root. This strong suction force limits water access to the roots and the effect is inflicted in the aerial parts of the plant.

3.2. Differential varietal responses to water deficit

The variance components of the main effects of varieties, water level and year and their interaction effects are presented in table 2. Results of the analysis of variance of the combined dataset indicated highly significant ($p < 0.001$) variety by stress-level interaction. The main effects of water levels, varieties and years were also inflicted significant effect on the three traits with significance level ranging from $p < 0.001$ to $p < 0.05$. This indicates that varieties are genetically very diverse for the traits and differently reacted to the imposed stress. The interaction of varieties with supplemented irrigation was very evident showing that selection of responsive varieties would increase water use efficiency in the drylands.

Table 2. Mean square values of days to maturity (DM), panicle length (PL) and grain yield (GY) from main effects and interaction between the stress and varieties

<i>Source of variation</i>	<i>D.f</i>	<i>Variates</i>		
		<i>DM</i>	<i>PL</i>	<i>GY</i>
Year	1	590.42 ^{***}	5.08 [*]	0.01 ^{ns}
Suppl. irrigation	2	387.6 ^{**}	401.38 ^{***}	5.87 ^{***}
Variety	14	95.36 ^{***}	31.66 ^{***}	0.38 ^{***}
Suppl. Irrigation × variety	28	5.4 ^{***}	6.21 ^{**}	0.07 ^{**}
Error (<i>sub-plot</i>)	28	1.1	2.38	0.03

(Note: *D.f* = degree of freedom, ^{ns} non-significant, ^{***} significant at $p < 0.001$, ^{**} significant at $p < 0.01$, ^{*} significant at $p < 0.05$).

3.2.1. Terminal Drought Adaptation Mechanisms in Tef

At severe stress level, those varieties with significant differences for days to maturity and panicle length between the mean of non-stressed plots and the severely stressed plots without significant loss in grain yield are considered to have drought escape and tolerance ability. Because the yielding potential of varieties does not varied significantly (Table 2), the effect of the factor year was omitted subsequent discussions. Deviations of mean performance of each variety due to the moderate and severe water stress from the standard (non-stressed) performance were presented in table 3. The analysis of the magnitude of deviation under severe stress condition was the base to understand adaptation mechanism of the varieties.

3.2.2. Plasticity in Maturity Time (Drought Escape)

As most crops, tef varieties grown under similar growing condition tend to show differences in maturity time due to varietal diversity for this trait. Considering the 2I (non-stressed) water level as conducive growing conditions where the genetic potential of the varieties expressed well, the studied varieties have shown about 14 and 13 days of maturity difference in 2011 and 2012, respectively (Fig 2). The varieties have expressed to some extent genotype by year interaction for days to maturity. In 2011, the earliest (≈ 85 days) matured variety was a local variety #11 (*Abat key*) while in 2012 it was an improved variety #5 (DZ-01-1285).

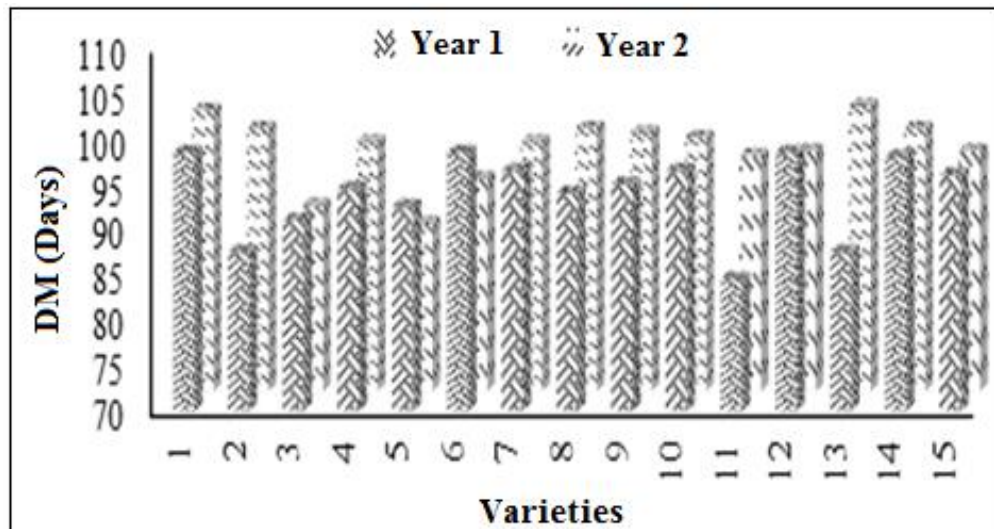


Figure 2. Varietal variation for days to maturity across years under normal growth conditions.

Similarly, the late maturing varieties were not the same for both years. Only four varieties took shorter days to mature in 2012 compared to their maturity date of 2011. Earliness is an important

drought escape attribute of tef, but significantly vary among varieties, and is, indeed, a major component of genotype by year interaction (G×E). Deviation in days to maturity of a particular variety due to the severe stress condition in comparison with the non-stressed condition ranged from 8 days for *AbatNech* to 2 for DZ-cr-37 (Table 3). Difference in maturity of the same variety under different water conditions at the same experimental site could demonstrate the possible existence of developmental plasticity in tef varieties. Early maturity crop varieties often escape drought because they complete the critical stages of crop growth prior to the setting of drought condition. In this study, varieties that have hastened their maturity time under drought condition by more than 5 days are considered as drought escapers. Furthermore, varieties which were not encountered significant yield loss due to the severe water stress (determined from treatment mean comparison) are nominated as drought tolerant.

Table 3. Mean values for days to maturity and grain yields of tef varieties under non-stressed and deviations from base performance due to mild and severe stresses

Variety	Days to maturity (days)				Gain yield ($t\ ha^{-1}$)				Possibly employed adaptation strategy
	Water conditions, the base (2I) & deviations from the base								
	Base	Δ_1	Δ_2	Δ_3	Base	Δ_1	Δ_2	Δ_3	
1	100.00	3.99	6.0	2.01	1.27	0.17	0.38	0.21	Escape, tolerance
2	93.50	1.49	1.8	0.26	1.34	0.28	0.79	0.51	Very susceptible
3	91.00	3.99	7.3	3.26	1.64	0.16	0.50	0.34	Escape
4	96.25	1.24	7.0	5.76	1.52	0.57	0.92	0.35	Escape, susceptible
5	91.75	0.74	3.0	2.26	2.08	0.71	1.20	0.49	Susceptible
6	96.25	1.99	6.5	4.51	1.20	0.19	0.39	0.20	Escape, tolerance
7	97.25	2.99	5.5	2.51	1.29	0.03	0.41	0.38	Escape, tolerance
8	96.75	0.99	3.3	2.26	1.07	0.35	0.62	0.27	Susceptible
9	97.00	1.99	2.8	0.76	1.27	0.42	0.59	0.17	Susceptible
10	97.50	1.49	3.0	1.51	1.51	0.60	0.95	0.35	Very susceptible
11	90.50	2.74	4.8	2.01	1.32	0.39	0.68	0.29	Susceptible
12	97.75	5.24	8.0	2.76	1.34	0.29	0.56	0.27	Escape
13	94.75	3.74	6.0	2.26	1.19	0.28	0.41	0.13	Escape, tolerance
14	98.75	2.99	6.8	3.76	1.35	0.40	0.51	0.11	Escape, susceptible
15	96.50	3.49	5.8	2.26	1.25	0.20	0.64	0.44	Susceptible
LSD _{int} (5%)	5.22				0.45				

(Note: LSD_{int} = least significance difference for the interaction effect; $\Delta_1 = 2I-II$; $\Delta_2 = 2I-RF$; $\Delta_3 = II-RF$).

Terminal drought escaping through early maturing by itself may not guarantee that the variety is useful for adaptation to drought conditions. Because the main purpose of crop production is the

final grain yield, substantial volume of yield has to be harvested for the target variety. A variety can be considered as useful if it possesses both earliness and good yielding ability to certain degree of its genetic potential. The yield of each tested variety from non-stressed plots (base yield) and deviations from the base under the two stress conditions was presented in table 3. The original genetic yielding potential of the fifteen tested tef varieties is significantly ($p < 0.001$) different (Table 2). Yield obtained for each variety from the twice supplemented plots was assumed to be its potential yield and deviations from this potential yield due to the two stress conditions was used to compare the varieties. Accordingly, variety DZ-01-1285 and DZ-01-196 showed the highest, 1.20 and 0.95t ha⁻¹ respectively, yield deviations due to severe stress. Expressed in terms of yield loss, severe stress has caused a yield loss of 57.7% and 62.9% in variety DZ-01-1285 and DZ-01-196, respectively. On the other hand, varieties DZ-01-974, DZ-01-899, DZ-cr-358 and *Berkayi* have incurred a yield loss of less than 40% because of the severe terminal drought. These varieties are actually regarded as terminal drought tolerant as the deviation of their yield due to the severe stress is not statistically significant (Table 3). With regard to temporal performance of the varieties, in 2011 the yield loss ranged from 16.7% to 79.4% while the loss magnitude ranged from 5.2% to 56.6% in 2012. The performance of the varieties greatly varied across years except for varieties DZ-01-974 and DZ-cr-358.

3.2.3. Reduction of Evaporative Surfaces

In agricultural terms, drought refers to a condition in which the amount of water available in the rooting zone is insufficient to meet the transpiration needs of the crop. Crop plants use various morpho-physiological adjustments to withstand the insufficient water conditions. In this study, the effect of water stress on panicle development of tef varieties was investigated and found that water stress limits the growth of tef panicle very significantly (Fig 3). The phenotypic variance ($R^2 = 21.5\%$) for panicle length is significant ($p < 0.001$) among the genotypes. The increase in variability ($R^2 = 33.1\%$) upon exposure of varieties to severe water stress (RF) presumably indicates that the varieties differentially reduce their panicle development, which is the active transpiring shoot part during post-anthesis stage.

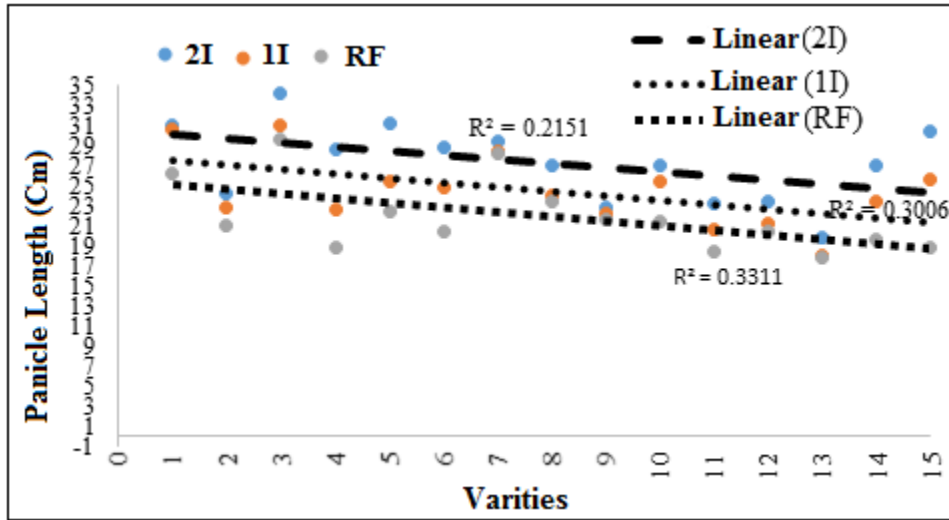


Figure 3. Sketch of mean panicle length of tef varieties for the three water regimes.

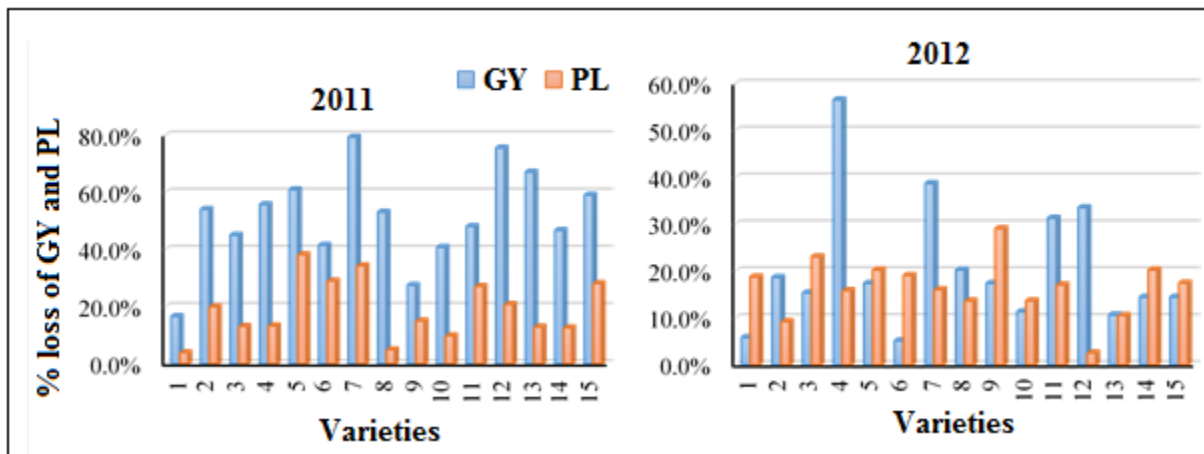


Figure 4. Grain yield loss and panicle length decrease under severe water deficit in relation to the unstressed performance.

Under water deficit conditions, decrease of shoot organs is the first process to occur as drought avoidance mechanism, before any reduction in biomass accumulation or stomatal conductance. The reduction in growth of the panicle of the 15 tef varieties increases as the severity of the stress increase (Fig 3). This reduction is, however, not the same in 2011 and 2012 (Fig 4). The figure presents the reduction in percent of panicle length of the 15 tef varieties. It is interesting to see that some varieties have proportional yield loss to the reduction in their panicle length under the severe water stress. The Pearson correlation analysis (*data not shown*) revealed that grain yield and panicle length strongly correlated ($r = 0.47$; $p < 0.001$). It seems that in some varieties

such as variety DZ-01-99, DZ-cr-358 and *AbatNech*, the amount yield loss is not proportion with the reduction in panicle length. In other cases, further reduction in panicle length tends to decrease the loss in grain yield probably due to reduction of surface evapotranspiration.

4. DISCUSSION

Constitutive morpho-physiological traits are inherited traits that are expressed both under well-watered and drought conditions. The genes controlling these traits can affect yield all levels of water stress conditions (Tuberosa, 2012). Different scholars have reported that early flowering as adaptation strategy (Vadez et al., 2012; Richards, 2006) to adapt terminal drought without considering the plasticity of phenological development merits. In arid and semi-arid areas where drought usually coincides with the grain filling stages, developmental plasticity between flowering and maturity times is rather more important. For such cases, phenotyping for day to maturity than days to flowering sounds perfect to evaluate the tolerance of crops to terminal drought. For this reason, days of maturity is considered as one of the traits for phenotyping crops for drought adaptation (Muñoz-Perea et al., 2007; Foster et al., 1995). The sensitivity of the different tef varieties to terminal drought is quite different (Table 3 and Fig 4) and as a result trigger different morpho-physiological mechanisms to adapt the effect of this drought. The reaction of the varieties ranges from escaping to tolerance.

Traditionally, tef is considered as drought tolerant crop and as a result used as a rescue crop in case other crops fail from early season drought. This usually puts tef in the category of less water demanding crops. Despite this fact, as the result of this study shows that the yield loss of tef incurred to terminal drought is very high (Table 3). For this reasons, targeting tolerance to terminal drought affecting tef during the grain filling is the major target for yield improvement under drought conditions. The final yield under stress condition is, in part, also determined by the yielding potential of the tested genotype, i.e. variety, plus some escaping mechanisms to the phenology (Vadez et al., 2012). This analysis revealed that the tested tef varieties are quite diverse in their reaction to terminal drought (Tables 2 and 3). Some of the tested varieties such as DZ-cr-387, DZ-01-99, DZ-cr-358, DZ-01-1681, *AbatNech*, *Berkayi* and *Kobo* have employed drought escaping mechanism with varying degree of associated yield loss.

Decreasing the growth of shoot parts such as leaf and branches could also be considered as drought avoidance mechanism, which occurs under water deficit conditions before any reduction

in biomass accumulation or stomatal conductance (Saab and Sharp, 1989). The potential of tef to decrease the functionality of active leaf area through leaf rolling or epinasty was previously confirmed (Mengistu, 2009). The current study revealed that this crop also decrease other evaporative surfaces which are active during the later growth stages. The panicle of tef is an actively growing part from booting to the final grain filling stages and is supposed to be the most actively transpiring part of the shoot. The degree of drought avoidance in plants is genetically dictated and varies even within a species (Parent et al., 2010; Welcker et al., 2007). In the current study, varieties DZ-01-99, DZ-cr-358 and *AbatNech* have significantly reduced the growth their panicle which assumed helped them maintain relatively higher grain yield under severe water stress condition. Previous studies also confirmed that different tef varieties reduce their panicle elongation to various degree under water stress (Abuhay, 1997). Reduction of panicle length presumably help the varieties to concentrate assimilates in the lower rachis for fast grain development rather than using assimilates for panicle elongation. The mechanisms, either escape or reduction in evaporative surfaces, that confer stress avoidance under terminal drought are usually associated with a reduced biomass accumulation and the final grain yield (Table 3; Fig 4).

5. CONCLUSION AND PERSPECTIVES

Genetic resources utilization to combat the effect of terminal drought will require a better understanding of the physiology and genetic basis of constitutive drought-adaptive traits. The result suggests that some phenotypic traits of tef such as days to maturity and panicle length are strongly but differentially influenced by the level soil water stress imposed during the reproductive stages. The different tef varieties, however, respond differently to the imposed water stresses indicating that the investigated traits are highly influenced by the interaction between varieties and water environments. Such phenotyping of crop varieties for drought-adaptive traits has been evidenced to overcome the devastating effects of terminal drought in different drought prone parts of the world. By similar analogy, phenotyping tef varieties for developmental plasticity has clued that the tested varieties appear have employ either escaping (early maturity) or decreased growth of panicle under severe water stress to overcome the severe effects of terminal drought. Two varieties, DZ-01-974 and DZ-01-899, have however possessed both escape and reduction of evaporative surfaces to overcome the devastating later stage water

deficit stress. The presence of tef varieties with drought escape, drought tolerance and susceptibility nature was revealed in this study. This triggers the need for phenotyping of larger collections of tef varieties for precise dissection of drought-adaptive traits in tef. This, in turn, will help to tailor varieties that better suited for drought prone farming systems.

6. ACKNOWLEDGEMENTS

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