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Allelopathic Potential of Teff Varieties and Effect on Weed Growth

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Abstract: Allelopathic potential of 10 teff varieties was assessed in laboratory experimentation (conducted in NIBIO, Norway), and determined with an agar-based bioassay using ryegrass and radish as model weeds. Field experiments were conducted in Tigray, Ethiopia during 2015 and 2016 to identify the most important agronomic traits of teff contributing to its weed competitive ability. A split plot design with three blocks was used considering hand weeding as the main plot and varieties as the subplot. Randomized complete block design (RCBD) with four blocks was used in the laboratory experiment. The highest potential allelopathic activity (PAA) and specific potential allelopathic activity (SPAA) were recorded from a local landrace with an average PAA value of 11.77% and SPAA value of 1.21%/mg respectively, when ryegrass was used as the model weed. 'Boset' had the highest average PAA value of 16.25% and an SPAA value of 1.53%/mg, when using radish as the model weed. The lowest PAA and SPAA values were recorded from 'DZ-Cr-387' when using ryegrass and radish as model weeds. Days to emergence, height, tiller no./plant, biomass yield, and PAA of the crop significantly contributed to the variance of the weed biomass, cover, and density. Hence, they were the most important agronomic traits enhancing the competitive ability of teff.

Keywords: Teff; weed; ryegrass; radish; allelopathy; potential allelopathic activity; weed root growth

1. Introduction

Teff (*Eragrostis tef* (Zucc.) Trotter) is among the oldest cereal crops in the tropical African region and is originated and more diversified in Ethiopia than in any other part of the world [1]. It is a C_4 plant classified under the family Poaceae, and genus Eragrostis [1]. It is the major cereal crop in Ethiopia in both production and consumption. It is consumed by more than 60% of the country's population on a daily basis [2]. The crop is not only adaptable to a wide diversity of agroclimatic conditions, but also has wide genetic variability encoding for a variety of agronomic traits [1,3]. Such a wide adaptation to different agroecologies exposes it to various weed species [1,3–7]. It faces challenges from weeds throughout its growing period that lead to decreased yields [8–10]. There are different cultural methods of weed control, most of which are included in agronomic practices with teff [11]. The most common include frequent tillage before sowing the crop, hand weeding, and to some extent, the use of post- and pre-emergence herbicides. Planting design, which includes planting density, row spacing, and orientation, can also be used as a method of weed management because it can enhance the crop's competitive advantage over weeds [12]. The evolution of herbicide-resistant weeds has become a bottleneck and thus calls for alternatives [13,14].

The use of competitive varieties is an interesting option for the nonchemical weed control method because it does not add any additional costs and does not create agronomic and environmental concerns. In contrast to the use of weed competitive potential of wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), and oat (*Avena sativa* L.) varieties [15], knowledge on the potential use of competitive teff varieties is very limited. Haftamu et al. [11] studied the competitive ability of teff varieties as well as their traits, e.g., canopy heights and tillering potential of different teff varieties. However, a potential link between the traits of teff varieties and their weed competitive ability was not investigated in that study. There have been a huge number of studies that illustrate the variation in competitive ability between varieties of different cereal crops such as wheat, oat, and barley [15]. They give many examples of traits, e.g., canopy height, early vigor, and release of different allelochemicals that contribute to increased suppressive ability against weeds.

There are many definitions for the word "competition", see e.g., in [16]. In this study, we include a specific kind of competition, form of interaction among plants, called allelopathy, which refers to plant released toxins. Allelopathy is an interference interaction among organisms (specifically plant species) through the release of allelochemicals that hinder the growth and development of another organism (plant species) living near to them [17,18]. This study mainly focused on the suppressive effect of one plant species (teff) on other plant species (weeds). Past studies have stressed the impact of allelopathy on various plant species on overall growth and performance of teff [19,20]. Phytotoxins are released by most plant species into the soil environment during four important processes—residue decomposition, volatilization, leaching, and root exudates, which may or may not be of benefit to other receptor plants (plants that receive allelochemicals during nutrient and water uptake from the soil) [18,21]. The presence of such phytochemicals may inhibit the proliferation of the roots of susceptible receptor plants and interrupts their life cycle through prevention of nutrient and water uptake. Allelochemicals can also hinder weed growth and development during crop production [18,22,23]. Cereal crops such as oat, corn, barley, and wheat have shown suppressive or allelopathic effects on weeds [22–26], but many of these have been transient or temporal. However, the use of different crop varieties that interfere with the root growth of weeds through exudation of allelochemicals [22,23,25] shows promising results. Bertholdsson found that early crop biomass and allelopathic activity of barley and wheat were the most important traits significantly contributing to their competitiveness against weeds [24] and also found that older landraces were most weed suppressive in laboratory and field assays.

Therefore, it is of paramount importance to identify teff varieties with weed suppressive potential through laboratory assays and field experiments and clearly define the most effective traits associated with weed suppression, which can be incorporated into integrated weed management systems.

The objectives of this study were (i) to uncover new knowledge about the allelopathic activity of teff varieties and (ii) to identify the most important agronomic traits of teff contributing to the competitive ability of the crop. We raised the following hypotheses:

1. There are differences in allelopathic activity between teff varieties.
2. Emergence and allelopathic activity are the two most important traits for teff's competitive ability against weeds.

2. Materials and Methods

2.1. Plant Materials

Ten teff varieties were used for the allelopathic experiment among which the nine of them were highly productive, adaptive, and widely used varieties. The remaining one was a local landrace. These varieties include Boset, DZ-01-1681, DZ-01-2675, DZ-Cr-387, DZ-01-974, DZ-Cr-385, DZ-01-354, DZ-Cr-358, Kora and local land race. More detailed descriptions of these varieties can be found in Haftamu et al. [11]. They were selected because they are highly preferred by the small-scale farmers of

Ethiopia for production. The following figure (Figure 1) displays photos of the most weed competitive teff varieties identified by Haftamu et al. [11].

(**A**) (**B**) (**C**)

Figure 1. Plots containing mature plants of some of the most weed competitive teff varieties. (**A**) DZ-Cr-387 (Quncho), (**B**) Kora and (**C**) Boset.

Ryegrass and radish were used as model weeds during the bioassay experiment. Ryegrass (*Lolium perenne cv. Mondiale; cv = cultivar*) was used as the model weed in Bertholdsson [24], and radish (*Raphanus sativus cv Cherry Belle*) was used in the experiments of Campbell [27] and Dennis [28]. Ryegrass is a grass (monocot) weed, whereas radish is a broadleaved (dicot) weed. Both ryegrass and radish were used as model weeds in the bioassay conducted by Espen Haugland and Lars Olav Brandsæter [29].

2.2. Part I: Detecting the Potential Allelopathic Activity (PAA) of Teff Varieties (Bioassay Experiment)

The varieties were tested for their PAA in the bioassay experiment. A randomized complete block design with four blocks replicated in time was used during the testing period. An agar-based bioassay was conducted using ryegrass and radish as model weeds. Our laboratory methods used during the period of the experiment were almost completely adopted from Bertholdsson [24] and Wu et al. [26]. The experimental process was performed in three steps.

2.2.1. Seed Germination of Teff Varieties and Model Weeds

Seed germination of teff and the model weeds (ryegrass and radish) was performed in the weed laboratory (NIBIO, Ås, Norway) (Figure 2). Petri dishes with litmus paper (grade 1 with 8.5 cm size Whatman litmus paper) was used to germinate the seeds and 2 mL water (which was determined in our preliminary study conducted before the start of the bioassay) was applied. Seeds of both teff and weed species were germinated in darkness at a room temperature of 20 °C for 3 days for teff and ryegrass and for 2 days for radish. All seed lots appeared to be well cleaned and hence were not further sterilized. Teff and model weed species were pregerminated and immediately prepared for transplanting into water-based agar.

Figure 2. Germination of teff and model weeds, ryegrass and radish, for the bioassay.

2.2.2. Transplanting of Seedlings of Teff and Model Weeds into Water Agar and Their Incubation in the Growth Chamber (Bioassay)

In the final bioassay, plastic tissue culture vials (Phytotech, 300 mL) were filled with 30 mL 1.5% water Agar (Agar Bacto), and twelve pregerminated teff seedlings were planted in a circle 1 cm away from the vial wall with six pregerminated perennial ryegrass or six radish seedlings transplanted in the center of the vial and 1 cm away from the teff seedlings (Figure 3). After completing transplanting of the seedlings of the weeds and 10 teff varieties, the agar vials were sealed and immediately placed in a growth chamber with a light/dark cycle of 12/12 h at a temperature of 20 °C during the day and 15 °C during the night and fluorescent light of around 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ [24]. This low light level was used to protect the roots of the seedlings from the effect of high light intensity.

2.2.3. Root Analysis and Weight Measurements

After 7 days, the agar vials along with the teff, ryegrass, and radish seedlings were withdrawn from the growth chamber. The roots of the model weeds were carefully removed from the agar manually and scanned to measure their area, length, volume, and diameter using an image analyzer (WINRHIZO ARABIDO 2013). Vials with only the weed species were used as controls. Roots of ryegrass and radish were dried at 60 °C for 48 h, and dry weight was measured after removal of the emerging shoots.

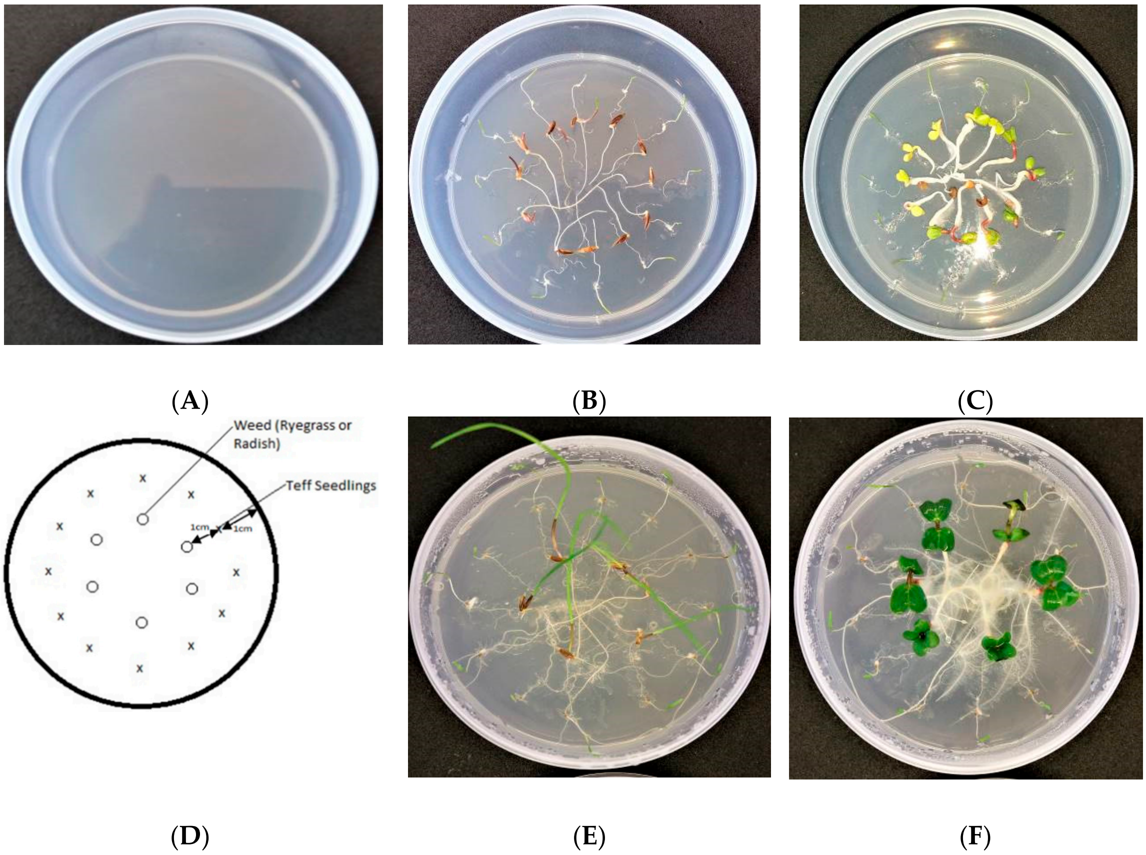

Figure 3. Seedling transplantation and growth of teff and model weeds in water agar. (**A**) Plastic tissue culture vials filled with 30 mL water agar; (**B**) Teff (DZ-01-1681) and ryegrass transplanted into water agar; (**C**) Teff (DZ-01-1681) and radish transplanted into water agar; (**D**) Transplanting design for teff and model weeds; (**E**) Teff (DZ-01-1681) and ryegrass after their incubation in the growth chamber for 7 days; (**F**) Teff (DZ-01-1681) and radish after their incubation in the growth chamber for 7 days.

2.3. Part II: Contribution of PAA and Other Teff Agronomic Traits on Weed Growth Dynamics

There are potential agronomic traits affecting the ability of teff varieties to suppress weeds and hinder their growth as explained in Haftamu et al. [11]. In this study, we have shown the contribution of these traits including PAA on the overall weed growth dynamics.

Data related to crop traits other than PAA were obtained from field experiments conducted in 2015 and 2016 at Mekelle and Axum research sites, which are found in the northern part of Ethiopia (Tigray). More information about these research sites and the field experiment design are well described in Haftamu et al. [11]. These crop traits were the days to emergence, days to heading/flowering, days to maturity, tiller number per plant, plant height, biomass yield, and grain yield. Days to 50% emergence, flowering and maturity were obtained by recording the dates when the teff plants covering 50% of the plot area emerged, flowered, and matured. Tiller number per plant and plant height were measured from 10 randomly selected teff plants from each plot. Tiller number per plant was recorded by counting the number of tillers in a single teff plant. Plant height (i.e., height of the teff plant from the node separating the root and shoot until the tip of the panicle) was measured using a *metre* and *centimetre* graduated flexible metal ruler. Biomass yield was obtained by recording the weight of the whole above ground part of teff plants in each plot.

Weed growth data included weed density, weed biomass and weed cover. Weed density and aboveground weed biomass were assessed three times before harvest in one randomly placed quadrate (25 cm × 25 cm) per plot. Weed density or infestation was estimated by counting the weed plants within the quadrate by weeding time (first, second, and third weeding). The space occupied by the crop and the most abundant weed species on all small plots was expressed as the percentage of ground coverage. The area covered by crop, weed species, and bare soil was summed-up to 100%. The biomass samples were dried at 65 °C for 48 h to determine the dry weight.

2.4. Data Analysis

Backward multiple regression (The backward multiple regression (i.e., backward elimination) began by considering all eight independent variables (i.e., emergence, heading, maturity, plant height, crop biomass yield, and PAA of teff on ryegrass and PAA of teff on radish) and ended with those without the estimates of the regression coefficients) and correlation analysis of the data from both bioassay and field experiments was conducted using SAS 9.4. Effects of the different teff varieties on root growth of ryegrass and radish during the bioassay experiment were correlated with each other in order to identify the variables that could best explain the allelopathic effect of the varieties. Potential allelopathic activity (PAA) was calculated based on the formula stated in the paper published by Bertholdsson [24] as PAA = (1 − A1/A2) * 100 where A1 is the weed root area in the presence of teff varieties and A2 is the weed root area without teff varieties. Based on PAA, the specific potential allelopathic activity (SPAA) was calculated as SPAA = PAA/weed root dry weight (this is the root dry weight of the model weed mixed with the specific teff variety based on which SPAA is calculated). PAA values can be positive or negative. Its values are positive when the weed root area is smaller in the presence of teff varieties than in their absence and negative when the weed root area is greater in the presence of teff varieties. Positive PAA values indicate that teff has an allelopathic effect on the model weeds and vice versa. The contribution of PAA and the other agronomic traits of teff (obtained from the field experiment) on weed growth was analyzed through regression analysis.

3. Results

All the teff varieties tested showed differences in their potential allelopathic effect on weeds. Days to emergence, days to heading, days to maturity, plant height, biomass yield, and PAA were the teff traits that contributed significantly to the variation in weed dry weight, cover, and density.

3.1. Part I: Detecting the Potential Allelopathic Activity (PAA) of Teff Varieties (Bioassay Experiment)

3.1.1. Allelopathic Effect on Ryegrass

The highest weed root length, root area and root dry weight of ryegrass were observed when co-cultivated with the teff variety DZ-Cr-387 (‘*Quncho*’) with average values of 19.4 cm, 0.57 cm^2, and 13.6 mg, respectively. Much lower root length, root area, and root dry weight of ryegrass were observed when co-cultivated with the teff variety DZ-01-2675 with average values of 15.3 cm, 0.4 cm^2, and 12.7 mg, respectively, and when co-cultivated with the local landrace with average values of 16.7 cm, 0.41 cm^2, and 8.5 mg, respectively, followed by DZ-Cr-358 and *Boset* (Figure 4). Teff varieties resulting in lower root diameter, root dry weight, root area, and root length of ryegrass had higher PAA and SPAA. The highest average PAA was recorded from the local landrace with an average PAA of 11.8% and an average SPAA 1.2%/mg and DZ-01-2675 with PAA 10.9% and SPAA 1.2%/mg. The lowest was from DZ-Cr-387 with an average PAA of 0.2% and an average SPAA of 0.1%/mg.

3.1.2. Allelopathic Effect on Radish

The highest radish root length, 28.5 cm, was recorded from DZ-Cr-387 followed by DZ-01-1681 with 25.3 cm and DZ-01-354 with 25.2 cm (Figure 5). Similarly, the highest value of root area was found in DZ-Cr-387 (1.1 cm^2) followed by DZ-01-1681 (1.05 cm^2) and DZ-01-974 (1.02 cm^2) (Figure 4). The highest radish root dry weight was recorded from DZ-01-1681 (12 mg) followed by DZ-Cr-358 (11.1 mg) and the local landrace (10.7 mg). Relatively lower root length (24.2 cm), root area (0.98 cm^2) and root dry weight (9.7 mg) were recorded from DZ-01-2675 (Figure 5).

The different teff varieties showed highly variable PAA and SPAA on radish (Figure 4). When comparing the PAA of the teff varieties, *Boset* had the highest PAA at 16.3% followed by DZ-01-2675 at 12.6% and *Kora* at 12%. The lowest PAA was from DZ-Cr-387 with a value of 1.8%. The teff varieties had also variability in SPAA where the highest value, 1.6%/mg, was observed from *Boset* followed by *Kora* and DZ-Cr-385 both having an average value of 1.5%/mg. The lowest SPAA value was from the variety DZ-Cr-387 (0.2%/mg). The variety DZ-Cr-387 (*Quncho*) showed consistently low suppressive effects on both ryegrass and radish i.e., this variety had lower phytotoxic effects than the other teff varieties.

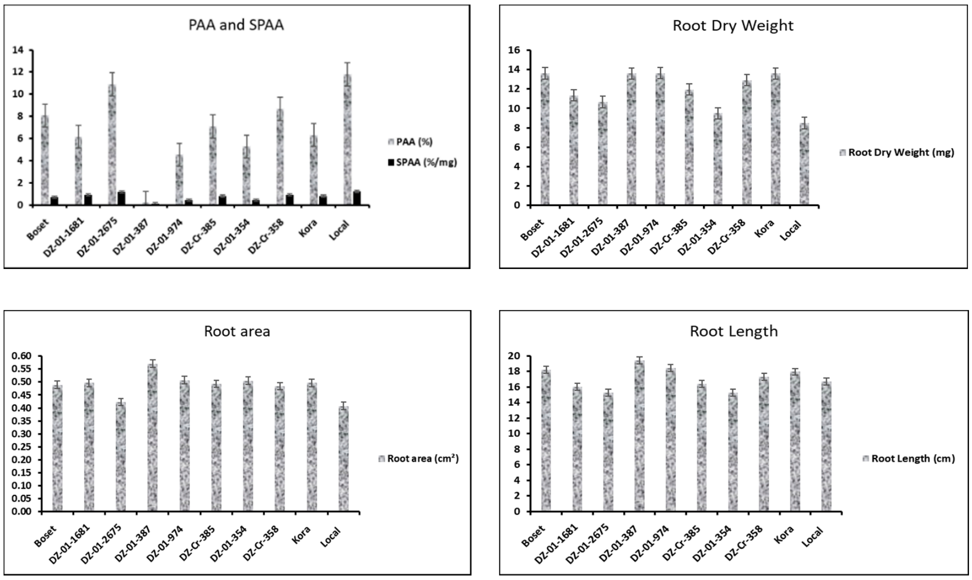

Figure 4. Potential allelopathic activity (PAA) and specific potential allelopathic activity (SPAA) of different teff varieties and their effect on root growth of ryegrass. **N.B.** Root area, root length, and root dry weight of ryegrass without teff varieties (control) were 0.61 cm^2, 20.6 cm, and 15.2 mg, respectively.

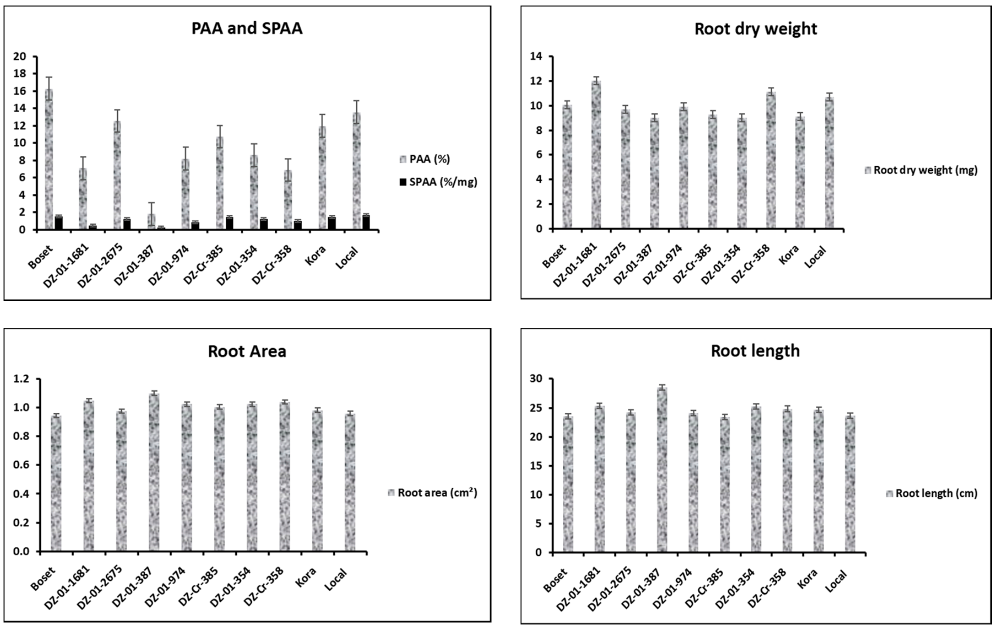

Figure 5. Potential allelopathic activity (PAA) and specific potential allelopathic activity (SPAA) of different teff varieties and their effect on root growth of radish. **N.B.** Root area, root length, and root dry weight of ryegrass without teff varieties (control) were 1.4 cm^2, 31.4 cm, and 14.3 mg, respectively.

3.2. Part II: Contribution of PAA and Other Teff Agronomic Traits on Weed Growth Dynamics

Relationships between Traits of Teff Varieties and Weed Assessments

Most of the weed assessments, i.e., weed biomass, cover, and density, had a significant positive strong correlation with the crop phenology, especially with days to emergence and days to heading (Table 1). This means that those teff varieties that were late to emerge and flowering faced strong weed competition during the vegetative growth period. Such a correlation was clearly observed spatiotemporally. The days to emergence showed a very strong positive correlation with weed biomass, density, and cover in 2015 in Axum (Table 1), but it did not have such a correlation in Mekelle in either year, except for weed cover in 2015. Heading showed temporal and spatial inconsistencies in its correlation with weed biomass, cover, and density.

For most of the sites and years, plant height, tiller number per plant, crop biomass yield, and PAA had a negative correlation with weed biomass, cover, and density, but the significance of their correlations was not spatiotemporally consistent (Table 1). Plant height and total tiller number per plant showed a significant strong negative correlation with weed density in 2016 in Axum. Teff tillering potential had a significant negative correlation with weed cover in Mekelle in 2016. Crop biomass yield had a significant negative correlation with the weed biomass, cover, and density. Though not significant in most of the locations and years, the PAA of the teff varieties showed negative correlation with all of these weed responses. Such a negative correlation of weed biomass, cover, and density with the PAA of teff varieties estimated using radish as a model weed was very consistent both spatially and temporally. Most of the agronomic traits of teff showed significant correlations with each other (Table A3 in Appendix A). Days to emergence had a significant strong negative correlation with the biomass yield of teff. Days to heading had a significant strong positive correlation with days to maturity and plant height, and days to maturity had a significant positive correlation with plant height and the tiller number per plant. Neither the PAA nor SPAA of teff showed a significant correlation with either of the agronomic traits of the crop.

The resulting estimated model from backward multiple regression analysis indicated that the traits of the different teff varieties, i.e., days to emergence, days to heading (flowering), days to maturity, plant height, number of tillers per plant, crop biomass yield, and PAA contributed to 70.3%–99.7% of the variation in weed biomass, cover, and density (Tables 2 and 3). Most of the traits had a greater effect in combination than separately. The contribution of crop emergence on the variance of the weed biomass, cover, and density was significant both spatially and temporally. The same trend was observed in crop biomass yield. Among the traits, emergence and crop biomass yield significantly contributed to the variance in weed biomass, weed cover, and weed density in 2015 in Axum (Tables 2 and 3). Days to heading, days to maturity, and number of tillers per plant significantly contributed to the overall variability of the weed biomass, cover, and density in 2016 in both of the experimental locations. The variance of such responses due to the difference in plant height of teff varieties was not consistent, except that it was significant for weed biomass in 2016 in Mekelle and for weed cover in both Axum and Mekelle in 2016. The PAA of teff varieties had a significant contribution to the variance in weed biomass, cover, and density (Tables 2 and 3) and contributed on average to 21.5%–28.2% of the variance in weed biomass, cover, and density.

Table 1. Coefficient of correlation between weed biomass, density, cover, and the traits of the different teff varieties.

	Weed Biomass				Weed Density				Weed Cover			
Crop Traits	**Axum**		**Mekelle**		**Axum**		**Mekelle**		**Axum**		**Mekelle**	
	2015	**2016**	**2015**	**2016**	**2015**	**2016**	**2015**	**2016**	**2015**	**2016**	**2015**	**2016**
Days to emergence	0.959 ***	−0.2065 ns	0.3689 ns	−0.359 ns	0.793 **	−0.2797 ns	0.3964 ns	0.3198 ns	0.8146 ***	0.7438 **	0.7719 **	0.4026 ns
Days to heading	0.2416 ns	0.3453 ns	0.3468 ns	−0.0485 ns	0.3302 ns	0.5559 *	0.6263 *	0.1626 ns	−0.0193 ns	0.2005 ns	0.6968 *	−0.2673 ns
Days to maturity	0.4421 ns	0.1602 ns	0.1601 ns	−0.1499 ns	0.3798 ns	−0.3127 ns	0.1395 ns	0.1959 ns	0.4056 ns	0.404 ns	0.2148 ns	−0.2251 ns
Plant height	0.2716 ns	0.1603 ns	0.0471 ns	−0.155 ns	0.4075 ns	−0.5705 *	−0.1936 ns	0.0465 ns	−0.0045 ns	−0.157 ns	−0.0735 ns	−0.3527 ns
Total tiller no. per plant	0.2716 ns	0.181 ns	−0.2087 ns	−0.3489 ns	−0.1073 ns	−0.524 *	0.2831 ns	−0.538 *	−0.0447 ns	0.0028 ns	0.0263 ns	−0.5266 *
Crop biomass yield	−0.8784 ***	0.421 ns	0.0258 ns	−0.5686 *	−0.7859 **	0.1844 ns	0.2452 ns	−0.4408 ns	−0.8632 ***	−0.8417 ***	−0.1496 ns	−0.5355 *
PAA $_{Monocot}$	0.1196 ns	0.0196 ns	−0.5306 *	−0.0223 ns	−0.0298 ns	0.0053 ns	−0.0533 ns	−0.0502 ns	0.0418 ns	0.3731 ns	0.0751 ns	0.464 ns
PAA $_{Dicot}$	−0.2807 ns	−0.2001 ns	0.155 ns	0.3154 ns	−0.322	0.1101 ns	−0.0845 ns	−0.504 *	−0.2412 ns	−0.0657 ns	−0.1511 ns	0.0797 ns
n	10	10	10	10	10	10	10	10	10	10	10	10

* significant at $p < 0.05$, ** significant at $p < 0.01$, *** significant at $p < 0.001$, ns not significant; PAA $_{Monocot}$ = Potential Allelopathic Activity of teff varieties estimated using ryegrass as the reference weed; PAA $_{Dicot}$ = Potential Allelopathic Activity of teff varieties estimated using radish (Cherry Belle) as the reference weed NB: each value of the correlation coefficient was squared to get the coefficient of determination (r^2) of each variables.

Table 2. Backward multiple regression analysis of the teff traits with weed biomass and cover as dependent variables and emergence, heading, maturity, plant height, crop biomass yield, and PAA of teff on ryegrass and PAA of teff on radish as independent variables.

Multiple Regression Models	**Weed Biomass**				**Weed Cover**			
Whole Model	**Axum**		**Mekelle**		**Axum**		**Mekelle**	
	2015	**2016**	**2015**	**2016**	**2015**	**2016**	**2015**	**2016**
R^2 (%)	98.65	77.05	70.29	98.24	99.69	95.82	89.52	83.59
p-value	<0.0001	0.1799	0.0691	0.0463	0.0108	0.0012	0.0024	0.0091
	p-values of independent variables							
Days to emergence	<0.0001 (179.2)	0.0524 (3.4)	0.0925 (55)	-	0.018 (−3.3)	0.0005 (0.4)	0.0004 (4.3)	-
Days to heading	0.0068 (29)	-	-	0.0039 (11)	-	-	-	-
Days to maturity	0.0061 (−13)	-	-	-	0.0096 (0.5)	0.0047 (−0.6)	-	0.017 (−0.3)
Plant height	-	0.0741 (−1.2)	-	0.0033 (−6.3)	0.0072 (−0.65)	-	0.0107 (−0.4)	-
Tiller no./plant	-	0.062 (9)	-	0.0186 (−33.8)	0.0973 (−2.1)	-	-	0.0034 (4.3)
Crop Biomass	-	0.0309 (0.01)	-	0.0225 (0.02)	0.0057 (−0.004)	-	-	0.0114 (0.002)
PAA $_{Monocot}$	0.051 (15.4)	-	0.0445 (38.2)	0.0691 (−2.8)	0.0319 (1.4)	0.0016 (0.6)	0.0831 (0.6)	-
PAA $_{Dicot}$	-	0.0591 (2.5)	-	0.0047 (7.4)	0.0493 (−0.66)	0.01 (−0.3)	-	-
n	10	10	10	10	10	10	10	10

(1) PAA $_{Monocot}$ = Potential Allelopathic Activity of teff varieties estimated using ryegrass as the reference weed; PAA $_{Dicot}$ = Potential Allelopathic Activity of teff varieties estimated using radish (Cherry Belle) as the reference weed. (2) R^2 with its corresponding *p*-value is from the final model of the backward regression. (3) The values in the brackets are the estimates of the regression coefficients for the independent variables significantly contributing to the variance of weed dry weight and weed cover. (4) The backward multiple regression began with all eight independent variables and ended with those without the estimates of the regression coefficients.

Table 3. Backward multiple regression analysis of the teff traits with weed density as the dependent variable and emergence, heading, maturity, plant height, crop biomass yield, and PAA of teff on ryegrass and PAA of teff on radish as independent variables.

Multiple Regression Models	Weed Density			
Whole Model	**Axum**		**Mekelle**	
	2015	**2016**	**2015**	**2016**
R^2 (%)	62.88	92.62	39.22	99.02
p-value	0.0062	0.0221	0.0527	0.0042
p-values of independent variables				
Days to emergence	0.0062 (50.4)	-	-	-
Days to heading	-	0.0043 (−20.7)	0.0527 (10.2)	0.0042 (18)
Days to maturity	-	0.0081 (24.1)	-	0.0038 (−21.8)
Plant height	-	-	-	-
Tiller no./plant	-	0.0463 (−19)	-	0.0061 (−49.7)
Crop Biomass	-	0.0448 (0.01)	-	0.0037 (−0.06)
$PAA_{Monocot}$	-	-	-	0.0134 (5.9)
PAA_{Dicot}	-	0.0075 (−9.6)	-	0.0013 (−11)
n	10	10	10	10

(1) $PAA_{Monocot}$ = Potential Allelopathic Activity of teff varieties estimated using ryegrass as the reference weed; PAA_{Dicot} = Potential Allelopathic Activity of teff varieties estimated using radish (Cherry Belle) as the reference weed; (2) R^2 with its corresponding *p*-value is from the final model of the backward regression. (3) The values in the brackets are the estimates of the regression coefficients for the independent variables significantly contributing to the variance in weed density. (4) The backward multiple regression began with all eight independent variables and ended with those without the estimates of the regression coefficients.

4. Discussion

Plants exhibit multiple interactions when growing among each other and such interactions include competition for soil resources such as water, nutrients, solar radiation and space. This competition includes an interference through chemical exudates emitted from plants to the soil. Crop plants and weeds can exhibit such interactions during their life cycle under field or laboratory conditions. Allelopathy is defined as the adverse effect of one plant on another through the production of Phytotoxins or allelochemicals, thereby impacting growth and development of neighboring plants [30]. Crop species show differences in their responses to weeds.

Many studies have shown that the use of competitive varieties can be an important tool for integrated weed management [15,31]. As already mentioned, there is little knowledge on the differences in competitiveness between varieties of teff and which traits of the different varieties might explain the differences in weed competitiveness. Apart from the study by Haftamu et al. [11], we have not found any studies showing the influence of different varieties of teff on weed growth. In this study, the weed dry-weight ranged from 150.11 g to 356.37 g per m^2 in unweeded plots between the most and the least (plus 137%) competitive teff varieties, representing two fold difference in weed suppression [11].

Studies have shown that cultivars within a cereal species emanate difference in allelopathic activity and that this trait can contribute to reducing weed interference [31]. The genotypic effect of a single crop species and its environment has also been shown to affect the release of allelochemicals and their effects over time [18]. Inhibition of root growth of weeds and other plant species is among the indicators of the allelopathic effects of crop plants [32–34]. At this time, we believe there are no research reports on the allelopathic effect of teff on different weed species. Most reports have focused on the allelopathic effect of certain plant species on teff [19,20,35–43]. For example, leaf extracts from different eucalyptus species and *Parthenium hysterophorus* had an effect on the germination and early growth of teff [19,20]. In our experiment, where we used a method that did not potentially allow competition for resources between teff and model weeds, we showed that the different teff varieties caused differential root growth of ryegrass and radish. Our first hypothesis, that there are differences in allelopathic activity between teff varieties, was therefore supported. This is consistent with the idea that genotypic variation can impact the allelopathic effect of crop species [18]. Among the tested teff varieties, the local landrace and the variety DZ-01-2675 were successful in reducing the root length, area, and dry weight of both ryegrass and radish. The PAA and SPAA can be used as parameters to express the allelopathic effect of crops on weeds [24,26]. Among all the varieties, the local landrace and DZ-01-2675 had relatively higher allelopathic effects on ryegrass because they had the highest PAA and SPAA values. On the other hand, the variety Boset had the highest allelopathic effect on radish followed by DZ-01-2675 and Kora. These are among the high-yielding teff varieties in Ethiopia [1,44]. However, the dominantly produced and high yielding variety widely grown in Ethiopia, DZ-Cr-387 (Quncho) [45], exhibited the least growth suppression on both ryegrass and radish model weeds.

From the field experiments conducted in Axum and Mekelle in 2015 and 2016, the most important agronomic traits affecting weed growth were days to emergence, days to heading, days to maturity, plant height, tiller number per plant, and crop biomass yield. As already described, the allelopathic potential of the teff varieties obtained from our laboratory experiments was among the important traits of the crop. Most of these traits showed a strong and significant correlation with weed biomass, cover, and density, and this is consistent with many other studies showing that crops with "early vigor", including early emergence, early flowering, and early maturity, often cause significant growth reductions of weeds [24,46]. Furthermore, many other studies have shown that taller plants [46,47] with higher tillering potential [48], higher crop biomass yield, and higher allelopathic effect [15,24,49,50] have higher competitive ability and cause reasonable reductions in weed biomass, cover, and density. Days to crop emergence is probably the main factor for crop competitive ability and the release of root exudates, i.e., allelochemicals [24]. Days to emergence was an important trait for explaining differences in weed interference between cultivars in our study. Therefore, our second hypothesis, that emergence and potential allelopathic activity are the two most important traits for teff weed competitive ability, was partly supported. However, not only the early vigor, but also the later growth stages of the teff varieties affected the biomass, cover, and density of weeds during teff production. Teff varieties that exhibit early emergence have the potential to compete with weeds for water and nutrients. Most of the early emerging varieties have early maturing habits and are mostly adapted to low to mid-altitude environments of Ethiopia characterized by high weed intensity [1,3,7,44,51]. As already stated above, the PAA of the teff varieties contributed on average from 21.5% to 28.2% of the variance in weed biomass, cover, and density. This suggests that this trait is particularly important in driving weed suppression and it is interesting to note that this mean is comparable to values found in spring barley in which the PAA in the model explained 12%–26% of the variance in weed biomass, although PAA was a less important trait in wheat compared to barley [24]. Another interesting finding in our study was that the local landrace has a high allelopathic potential. This is similar to the findings on barley observed in experiments conducted in Sweden [31]. In this study, Bertholdsson concluded that "the allelopathic activity of barley probably originated from different landraces, and in most cases from a specific landrace from the Swedish island of Gotland. We suspect that more than 100 years of selection and breeding have resulted in a dilution of the genes from landraces and consequently a declining allelopathic activity". Although we believe that the method we have used in the present study, for estimating the allelopathic potential, is proven and reliable [29], it is also crucial to be aware that this part of the study was performed in laboratory petri dishes and not under field conditions. Such factors as osmotic potential, as discussed by Haugland and Brandsaeter [29] who used radish and ryegrass as test species, and nutrient or microbial interactions may influence results of laboratory petri dishes experiments.

In this study, teff phenology significantly explained the variance in weed biomass, cover, and density, thus confirming these traits' contribution to reducing of the overall performance of weeds under field conditions during production. The other agronomic traits, i.e., plant height, tiller no./plant, crop biomass, and allelopathic effect of teff contributed to the competitive ability of the crop as observed during the study period and explained more than 90% of the variance in the weed responses. We found temporal and spatial variability of the allelopathic effect of teff varieties, which might indicate the impacts of environmental factors on the PAA of crops [18]. Generally, the strong correlation between the weed responses and the agronomic traits of the different teff varieties indicated that these are the important traits explaining the potential competitive ability of teff during production and explaining more than 98% of the variance in weed performance under field conditions.

5. Conclusions

All of the teff varieties differed in allelopathic potential and inhibited early root growth and development of both monocot and dicot weeds.

The weed suppressive effects of teff had a conspicuous role in impacting weeds during their late stages and were able to affect their biomass, cover, and density.

In addition to the allelopathic effect, emergence and crop biomass yield were the most important agronomic traits contributing on the ability of teff to suppress weeds and inhibit their growth, although the contribution of plant height and tillering potential was also important. Additional field experimentation to evaluate the impacts of teff varietal competition and/or allelopathy will be valuable for sustainable weed management in teff.

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Appendix A

Table A1. Pearson correlation of the responses of ryegrass to the allelopathic effects of teff.

	Root Length (cm)	**Root Area (cm^2)**	**Root Diameter (mm)**	**Root Volume (cm^3)**	**Root Dry Weight (mg)**
Root length (cm)	1	0.9239 0.0001	−0.5848 0.0758	0.6483 0.0426	0.57582 0.0815
Root area (cm^2)	0.92394 0.0001	1	−0.3229 0.3627	0.7592 0.0109	0.48459 0.1558
Root diameter (mm)	−0.58483 0.0758	−0.323 0.3627	1	−0.2644 0.4603	−0.16693 0.6448
Root volume (cm^3)	0.64831 0.0426	0.7592 0.0109	−0.2644 0.4603	1	0.44691 0.1954
Root (dry weight (mg)	0.57582 0.0815	0.4846 0.1558	−0.1669 0.6448	0.4469 0.1954	1

Table A2. Pearson correlation of the responses of radish to the allelopathic effects of teff.

	Root Length (cm)	Root Area (cm^2)	Root Diameter (mm)	Root Volume (cm^3)	Root (Dry Weight (mg)
Root length (cm)	1	0.8388 0.0024	−0.8121 0.0043	0.3109 0.3819	−0.1913 0.5966
Root area (cm^2)	0.83882 0.0024	1	−0.3893 0.2662	0.7674 0.0096	0.01436 0.9686
Root diameter (mm)	−0.81207 0.0043	−0.389 0.2662	1	0.2546 0.4777	0.43235 0.2121
Root volume (cm^3)	0.31092 0.3819	0.7674 0.0096	0.2546 0.4777	1	0.19908 0.5814
Root dry weight (mg)	−0.19126 0.5966	0.0144 0.9686	0.4324 0.2121	0.1991 0.5814	1

Table A3. Pearson correlation of the agronomic traits of teff.

	Emergence	Heading	Maturity	Plant Height	Tiller No. Per Plant	Biomass Yield (kg/ha)	PAA_{rye}	$SPAA_{rye}$	PAA_{rad}	$SPAA_{rad}$
Emergence	1	0.56923 0.0859	0.58938 0.073	0.24164 0.5012	0.56447 0.0891	−0.79402 0.0061	−0.03352 0.9268	−0.124 0.7329	−0.3327 0.3475	−0.00824 0.982
Heading	0.56923 0.0859	1	0.93377 <0.0001	0.83025 0.0029	0.59615 0.0689	0.00091 0.998	−0.26368 0.4617	−0.23276 0.5175	−0.5653 0.0886	−0.149 0.6812
Maturity	0.58938 0.073	0.93377 <0.0001	1	0.73715 0.015	0.65183 0.0411	−0.0289 0.9368	−0.08545 0.8144	0.00143 0.9969	−0.4591 0.182	−0.07745 0.8316
Plant height	0.24164 0.5012	0.83025 0.0029	0.73715 0.015	1	0.43478 0.2092	0.20518 0.5696	−0.00891 0.9805	−0.04849 0.8942	−0.2027 0.5743	0.14782 0.6836
Tiller no. per plant	0.56447 0.0891	0.59615 0.0689	0.65183 0.0411	0.43478 0.2092	1	−0.32473 0.3599	−0.02873 0.9372	0.05773 0.8741	−0.5719 0.0841	−0.41598 0.2318
Biomass yield (kg/ha)	−0.79402 0.0061	0.00091 0.998	−0.0289 0.9368	0.20518 0.5696	−0.32473 0.3599	1	−0.16876 0.6412	−0.01427 0.9688	0.03512 0.9233	−0.07146 0.8445
PAA_{rye}	−0.03352 0.9268	−0.26368 0.4617	−0.08545 0.8144	−0.00891 0.9805	−0.02873 0.9372	−0.16876 0.6412	1	0.94648 <0.0001	0.75023 0.0124	0.70771 0.022
$SPAA_{rye}$	−0.124 0.7329	−0.23276 0.5175	0.00143 0.9969	−0.04849 0.8942	0.05773 0.8741	−0.01427 0.9688	0.94648 <0.0001	1	0.61775 0.057	0.5442 0.1039
PAA_{rad}	−0.33272 0.3475	−0.5653 0.0886	−0.45908 0.182	−0.20272 0.5743	−0.5719 0.0841	0.03512 0.9233	0.75023 0.0124	0.61775 0.057	1	0.8805 0.0008
$SPAA_{rad}$	−0.00824 0.982	−0.149 0.6812	−0.07745 0.8316	0.14782 0.6836	−0.41598 0.2318	−0.07146 0.8445	0.70771 0.022	0.5442 0.1039	0.8805 0.0008	1

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