Root architectural and morphological traits of *Eragrostis tef* under altered nitrogen availability and their relation to shoot traits

Master thesis, double degree - European Master in Organic Agriculture and Food Systems

Specialization at BOKU - Organic Agriculture in Tropical and Subtropical Environments
Specialization at AU - Organic Agriculture and Crop Science

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Affidavit of master thesis work

I Mads Rønby Priess Sørensen hereby declare that I am the sole author of this work "Root architectural and morphological traits of Eragrostis tef under altered nitrogen availability and their relation to shoot traits"; no assistance other than that permitted has been used and all quotes and concepts taken from unpublished sources, published literature or the internet in wording or in basic content have been identified with precise source citations.

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Århus 4/06/2021

Abstract

Teff (Eragrostis tef (Zucc.) Trotter is considered one of the most important food crops in Ethiopia. However, teff yields generally remain low. Roots play a vital role for the plant in both water and nutrient acquisition, and it is commonly acknowledged that root shoot interactions of crops are related to overall plant functionality, grain yield and quality. Therefore, a better understanding of teff root architecture and morphology, in relation to shoot traits under suboptimal agronomic conditions, could be useful for future breeding programs. In this study six genotypes, i.e., Addisie, Alba, Balami, Beten, T10 and T11, were cultivated in a greenhouse experiment under altered nitrogen conditions. Several, architectural and morphological root traits were characterized and tested for correlations between and within root traits and shoot traits. Significant effects of treatments and genotypes were observed for all shoot traits were with a general pattern of higher values under high nitrogen conditions. Total belowground biomass and seminal root count increased for certain genotypes, when exposed to higher nitrogen supply, however vertical root distribution was unaffected by altered nitrogen levels, but varied significantly between several genotypes. In terms of root shoot interactions, root shoot ratios were mainly affected by increased aboveground biomass, as no correlation between belowground biomass and root shoot ratios were detected. Morphological root traits were not significantly affected by altered nitrogen levels but differed between the genotypes. Moreover, morphological root traits were independent from both architectural root traits and shoot traits; however, negative correlations were found between specific root length and root diameter. In sum, this study provided a comprehensive characterization of teff root traits, showcasing, however, a greater plasticity of teffs' shoot traits compared to root traits in relation to nitrogen availability.

Keywords: Architectural roots, Eragrostis tef (Zucc.) Trotter, Ethiopia, Nitrogen, Root morphology, Teff.

Zusammenfassung

Teff (Eragrostis tef (Zucc.) Trotter) gilt als eines der wichtigsten Getreide in Äthiopien. Allerdings sind Teff-Erträge in der Regel niedrig. Die Wurzeln spielen eine wesentliche Rolle für die Wasser- als auch Nährstoffaufnahme der Pflanze, und es wird gemeinhin anerkannt, dass die Wurzel-Spross-Wechselwirkung von Getreide eine große Auswirkung auf Funktionalität der Pflanze, im Allgemeinen, uns insbesondere den Kornertrag und -qualität hat. Daher könnte ein besseres Verständnis der Wurzelarchitektur und Morphologie des Teffs, und die Veränderlichkeit unter suboptimalen agronomischen Bedingungen, für zukünftige Züchtungsprogramme nützlich sein. In dieser Studie wurden sechs Genotypen, i.e. Addisie, Alba, Beten, Balami, T10 and T11, im Gewächshausversuch unter veränderten Stickstoffdüngungen kultiviert. Mehrere architektonische und morphologische Wurzeleigenschaften wurden beschrieben und auf Korrelation zwischen und innerhalb der Wurzeleigenschaften und mit dem Spross geprüft. Signifikante Ergebnisse von Behandlung und Genotypen wurden bei allen untersuchten Eigenschaften festgestellt, allgemein zeigten sich höhere Werte unter höherer Stickstoffversorgung N+. Die unterirdische Biomasse und Anzahl der Seminalwurzeln erhöhte sich bei bestimmten Genotypen unter N+, jedoch blieb die vertikale Wurzelverteilung unverändert und durch den Genotype bestimmt. Das Wurzel-Spross-Verhältnisse wurde vorwiegend durch eine veränderliche oberirdische Biomasse beeinflusst. Morphologische Merkmale des Sprosses waren nicht signifikant von veränderten Stickstoffwerten beeinflusst, aber unterschieden sich zwischen den Genotypen. Zudem waren morphologische Wurzeleigenschaften sowohl unabhängig von architektonischen Wurzelmerkmalen als auch Eigenschaften des Sprosses. Negative Korrelationen zwischen Wurzellängen und Wurzeldurchmessern bestanden. Abschließend lässt sich sagen, dass diese Studie eine umfangreiche Charakterisierung der Wurzelmerkmale von Teff bietet. In Bezug auf die Stickstoffverfügbarkeit weisst Teff eine größere Plastizität der oberidischen merkmale im vgl. zu den Wurzelmerkmalen auf.

Schlagwörter: Architektonische Wurzeln, Eragrostis tef (Zucc.) Trotter, Stickstoff, Teff, Wurzelmorphologie, Äthiopien.

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1 Introduction

Teff (Eragrostis tef (Zucc.) Trotter; also known as “tef”, “Williams lovegrass” or “annual bunch grass”) is a major cereal crop with origins in Africa’s horn, in the countries of Ethiopia, and Eritrea. Archaeological studies have traced the cultivation of teff to the times of the early Aksumite kingdom of ancient Ethiopia 50 years BC, however, some claim teff was domesticated as early as 4000 BC by the pre-Semitic Ethiopians (D’Andrea, 2008; Stallknecht, 1997). Teff belongs to the Phocaea, sub-family Eragrostoidae, and is utilizing C4 photosynthesis as common for crops cultivated in tropical and subtropical environments. The harvestable parts of teff used for human consumptions are the tiny grains, with a thousand kernel weight of just 0.264 g, emerging from the panicle; however, the straw is also used for fodder and house building (Assefa et al., 2015; de Oliveira do Nascimento et al., 2018; Kakabouki et al., 2020). Today, teff is considered one of the most important crops in Ethiopia and the wider Easter African area. Teff household consumption from both own production and purchased grains is on average 7.5 kg per week, amounting to 31 % of total cereal consumption in Ethiopia (Mottaleb & Rahut, 2018). Teff is the main ingredient used for making the stable food teff injera, which is a sour fermented pancake, widely consumed. Numerous health benefits relate to the consumption of the teff injera, as it contains high amounts of minerals, such as calcium, zinc, and iron in particular (Abebe et al., 2007; Gebru et al., 2020; Mohammed et al., 2019). With the ongoing food and nutrition crisis in the region, the nutritional value of teff has been proposed as a tool to achieve several of the United Nations sustainable development goals (SDGs), such as SDG 1 (no poverty), SDG 2 (zero hunger), and SDG 3 (good health and well-being) (FAO, 2020; Golmohamadi et al., 2020). Moreover, teff is becoming increasingly popular outside of East Africa. It is especially praised as a superfood and a substitute for other cereals due to its gluten-free properties (Dingeo et al., 2020; Güngörmüşler et al., 2020; Homem et al., 2020).

Despite the importance of teff, however, yields generally remain low. For the Ethiopian grain growing season (meher) from May to September, the post-harvest survey of 2019-2020 estimated that teff was grown by 7.1 million farmers, on 3.1 million ha some 24 % of total cultivated grain crop area, with an actual yield of 5.7 million tons—amounting to 1.8 tons ha-1 (CSA, 2020). This is a substantially lower yield than other stable crops cultivated in Ethiopia from the same period, such as maize and wheat, grown on 17.6 %

and 13.9 % of cultivated grain crop area, and yielding 4.3 tons ha-1 and 3.1 tons ha-1 respectively (CSA, 2020). The low yields of teff are usually attributed to management practices and lodging. Traditionally teff is broadcasted during sowing, however, Mihretie et al., (2020) point to the fact, that under row planting teff performs significantly better. In fact, Birhanu et al., (2020) reported yields ranging between 1726.2 kg ha-1 to 2868.8 kg ha-1 depending on variety, while employing row planting in combination with irrigation and optimal fertilizer conditions. Despite these findings, the gap between potential and actual yields prevails in Ethiopia. Although adequate application of fertilizers evidently influences teff yields, the constraints of economic resources, fertilizer prices, and a lack of knowledge on application rates and management, are key components that prevent small-hold farmers, from optimizing their production systems (Assefa, 2018; Birhanu et al., 2020; Fikadu et al., 2019; Girma et al., 2012). In the perspective of the G × E × M concept, that is the interactions between genetics, environment and management, suggested by Hatfield & Walthall, (2015), it is argued that the genetic potential of a crop is a powerful tool when combatting yield gaps. For teff, research and organized breeding programs began in the mid-20th century and focused on pure line breeding for desired traits. Several thousand accessions of teff varieties exist, originating from indigenous germplasm. Moreover, landraces adapted to several different agroecological zones throughout Ethiopia are used in breeding programs (Assefa et al., 2015; Cheng et al., 2017; Woldeyohannes et al., 2020). That said, research on teff generally surrounds its nutritional benefits, management methods, and the preventing of lodging; however, from an agroecological viewpoint, trait-based characterizations of shoot physiology and morphology, and root system architecture interactions, are interesting for improving crop performance (Abalos et al., 2019; Paez-Garcia et al., 2015). It is commonly acknowledged that aboveground plant traits are correlated to the functionality of the plant. Specific leaf area (SLA) is correlated with the lifespan of the leaf among numerous species (Reich et al., 1992). In turn, correlations between SLA, and grain yield, have been used in breeding models to predict grain yields in different wheat genotypes (Asseng et al., 2003). Leaf traits such as SLA are part of the framework called leaf economic spectrum (LES), a tool used to evaluate plant nutrient acquisition strategies. Since roots play a vital part in sustaining the integrity and performance of a plant, a framework considering root shoot interactions, the resource economic spectrum

(RES), taking root traits and their functionality into account, has been proposed (Mommer & Weemstra, 2012; Reich, 2014). Not only do roots act as anchorage points for the plant, but they are also responsible for the water uptake and nutrient acquisition of nutrients such as nitrogen, phosphorus, and potassium in addition to micronutrients (Evert & Eichhorn, 2013). Thus, going below ground and investigating root traits of crops is becoming increasingly of interest, and herein lies a great potential for crop improvement (Paez-Garcia et al., 2015; Schneider & Lynch, 2020). Studies on other grain crops have investigated the relationship between shoot and root morphology and architecture (Atta et al., 2013; Jian-chang et al., 2012; Kanbar et al., 2009; Shangguan et al., 2015). However, there are yet, to the best of our knowledge, no comprehensive studies on teff root traits and potential root shoot interactions. A better understanding of teff root architecture and morphology, in relation to aboveground traits, is urgently required to better understand its ecophysiology and thus performance under suboptimal agronomic conditions.

Bardgett et al., (2014) divide root traits into four categories: architectural, morphological, physiological, and biotic of which this study will concentrate on certain architectural and morphological traits and how these potentially correlate with aboveground traits. It is commonly accepted that one of the most important morphological root traits related to root exploration is specific root length (SRL). SRL represents the ratio of root length per mass invested by the plant and is also regarded as a belowground analogue to the aboveground SLA (Bardgett et al., 2014; Corneo et al., 2017b). Two other prominent morphological root traits connected to SRL are root tissue density (RTD), which is the ratio between mass and volume, and root diameter (RDIA). Consequently, a high SRL and the innate advantage in soil exploration come at the “cost” of either low RTD or RDIA, or indeed low RTD and RDIA, resulting in fragile thin roots prone to a short lifespan and vulnerable to foraging herbivores and diseases (Birouste et al., 2014). Where root morphological traits describe characteristics for individual roots, root architectural traits describe characteristics of the spatial configuration of the whole root system (Bardgett et al., 2014). Important architectural root traits that have been linked to root exploration are i.e., the number of seminal roots, and the vertical root distribution (Doussan et al., 2003; Kemper et al., 2020). In monocotyledons such as grasses, seminal roots are considered embryonic roots that develops from the seed and contrast the roots originating from basal and upper parts of the shoot (Freschet et al., 2021). Vertical root distribution, which describes the root biomass at different depths through the soil column, provides information on the shallowness of the root system. A common measure for vertical root distribution is the regression coefficient β, derived from the model $Y=1-\beta d$ proposed by Gale & Grigal, (1987). By calculation cumulative root fractions, information on total belowground biomass (BGBM) can then be used to calculate the root to shoot ratio (R:S), when combined with total aboveground biomass (AGBM), which in turn gives a measure of the biomass allocation between shoot and root.

Knowledge of how crops react under different stresses such as under altered nitrogen availabilities, and where photosynthetic assimilates are allocated in the plant are argued to be key when planning breeding programs (Schneider & Lynch, 2020; Tracy et al., 2020). To this end, a better understanding of teff root shoot interactions could give precedence for traits to be targeted in future teff breeding programs.

Therefore, it is the goal of this study to provide an in-depth characterization on root traits and trait interactions above and belowground among several genotypes of Eragrostis tef when cultivated on altered nitrogen availabilities. In specific, the objectives are to:

(i) Determine the variability of root morphology and architecture based on the characterization of specific root traits of six genotypes of Eragrostis tef; hereunder four cultivars and two landraces.

(ii) Evaluating patterns of root trait plasticity of teff plants when grown under altered nitrogen environments; high (N+) vs. low (N-) nitrogen availability.

(iii) Identifying correlations between and within root traits and aboveground traits.

2 Material and Methods

2.1 Experimental design and growth conditions

A greenhouse experiment was initiated from May 22nd to September 3th 2020, at the research facility IFA-Tulln, Department für Agrarbiotechnologie (48°19'05.1" N, 16°03'58.2" E), about 45 km outside Vienna, Austria. The greenhouse was a tunnel-type plastic-foil greenhouse, with entrances in a north to south direction. The sides of the greenhouse were layered with an insect net on the inside so that the outside plastic foil could be opened on especially hot days. Climatic conditions were measured with a WatchDog data logger (Spectrum®Technologies, Inc., Aurora Illinois, America) placed 30 cm above the soil at a total height of 140 cm. The temperature during the growing period ranged between 23-38.7°C with a mean temperature of 30.2°C. Relative humidity ranged between 34-63 % with a mean of 39.8 %. Solar radiation was not measured in this period, however at the same location, Zhao et al., (2016) measured the sum of solar radiation as 13.28 MJ m^{-2} day^{-1}, with a maximum of 27.41 MJ m^{-2} day^{-1} on July 1st. Photoperiod was at seeding 15.5 hours and at harvest 14.5 hours. Due to tight restrictions on the export of teff seeds from Ethiopia, germplasm was kindly provided by the U.S. National Plant Germplasm System (USDA NPGS; order # 32648). Out of 25 eligible genotypes, 4 cultivars and 2 landraces were chosen based on a pre-experiment on contrasting root parameters of seedlings growing in the high-throughput phenotyping platform 2D-RSAT (Nottingham, UK) (Lorenz, 2021). The landraces originate from different agro-environmental conditions in Ethiopia (Table 1).

Table 1 Genotypes obtained from U.S. National Plant Germplasm System (USDA NPGS; order #32648). Genotypes are listed with their NPGS codes, their name, status and agro-ecological zone for the landraces. Moreover, number of samples, n per treatment per genotype, are listed.

NPGS code	Genotype name	Origin	Improvement Status	Agro-ecological zone	Treatment N+, n	Treatment N-, n
PI 524434	Addisie		Cultivar		15	15
PI 524435	Alba		Cultivar		14	13
PI 524436	Balami		Cultivar		15	15
PI 524437	Beten		Cultivar		13	15
PI 494243	T11	Kumbi	Landrace	warm/semi arid	15	12
PI 494239	T10	Jimma	Landrace	cool/humid	14	13

The teff plants were grown in PVC pipes (growth columns), arranged into a randomized block design with 15 blocks positioned in a north to south direction. Each block had two replicates of each genotype, thereby representing two nutrient treatments per block adding up to a total of n=180 plants in the experiment. The growth columns had the dimensions: height 110 cm, diameter 20 cm, and volume of ~34 dm^3. The columns were lined with a black plastic liner with corresponding dimensions to facilitate root retrieval, and with a perforated bottom for water drainage (Kashiwagi et al., 2005; Zhao et al., 2016). The bottom of the growth column was sealed, but with a 5 mm hole for water drainage. The growth medium consisted of a 1:3 mixture of low fertile loamy agricultural soil from the vicinity of the research station in Tulln, and coarse quartz sand, filled into the column until 10 cm below the top of the column. The bottom 5 l of the growth columns consisted of pure coarse sand to facilitate drainage. Soil pH was 7.87, measured with a pH electrode in a 0.01mol $CaC1_2$ solution.

All genotypes were pregerminated in 1-liter transparent plastic bags. Teff seeds were sowed in the same 1:3 soil sand mixture as in the growth columns, approximately 3 mm below ground. Two seeds per genotype, per repetition, were sowed in order to enhance the probability of germination. After sowing, each bag received water, and before the bag was closed to prevent evaporation. Three days after sowing all seeds from genotype Alba had germinated, and six days after sowing the remaining genotypes had germinated (data not shown). On the 1st of June, one of each germinated seedlings per bag was transplanted to the growth columns. Transplanting was done by hand with a plant shovel, and a 10 cm deep hole was dug in the growth columns. Carefully the sandwich bags were sliced open, and the seedlings were removed from the bags by shovel in order to keep the soil around the roots and not disturb the already established roots. The seedling with soil core was placed in the hole and gently watered.

2.2 Nitrogen treatments

Two nutrient treatments were established per block, one with high nitrogen denoted as "N+", and one with low nitrogen, denoted as "N-". As fertilizer the plants were given Hoagland's solution with KNO_3, $NH_4H_2PO_4$, $Ca(NO_3)_2$, $MgSO_4$, micronutrients, and with FE-EDTA as chelate, see supplementary table in the appendix (Table S1). Hoagland's solution is a well-recognized fertilizer solution that has previously been used in studies with cereals (Hoagland & Arnon, 1950; Huang et al., 1994). Six repetitions per block were given a treatment with 75% diluted Hoagland solution N+, with the above-mentioned chemicals. The other six replicas also received a 75% diluted treatment N-, although with a reduced nitrogen level. In order to create the altered nitrogen availabilities, the N- treatment was further diluted. KNO_3 was diluted to 10 %, $NH_4H_2PO_4$ and $Ca(NO_3)_2$ were substituted with KCl and KH_2PO_4 to balance potassium and phosphorus. ($CaSO_4$) H_2O_2 was added to balance calcium, see supplementary table for details (Table S1). Thereby each of the fifteen blocks of twelve teff plants had six plants receiving an N+ treatment, and six teff plant receiving a N- treatment, however not all plants per block survived until harvest and samples per treatment ranged between 12-15 (Table 1). The plants were given 100 ml of their respective fertilizer treatment weekly. Apart from fertilizer the plants received water via a drip irrigation system twice a day for 10 minutes per irrigation round, with a water flow of 2 liter per hour. The first few weeks of the growth period were especially hot, and a complimentary mist system was installed in order to prevent the seedlings from drying out.

2.3 Harvest

Harvest started on the 12th of August, i.e., 51 days after sowing (DAS), while the teff plants were in their vegetative stage. Harvest was done block-wise, and the last block was harvested at 73 DAS. Upon harvesting a block, the individual plants were measured from the base of the main shoot to the tip of the flag leaf. Hereafter, the plant was cut 1 cm from the soil for the seminal roots to stay connected to the crown. Tillers and main shoot were collected and imaged (Figure 1). Hereafter, they were put in paperbacks and brought back to the lab for further analysis.

Extraction of the roots followed that similar greenhouse experiments (Kashiwagi et al., 2005; Zhao et al., 2016). The columns were placed horizontally on top of a table with a net as a tabletop. By hammer and screwdriver, the bottom cap was removed so that the inner plastic could slide out. In order to investigate root distribution in the soil column, the back was cut open in intervals of 20 cm counting from the top down. Every section of the soil column was gently rinsed with water, in order to expose the roots. After rinsing, the root samples from each level were placed in water-filled bags and brought back to the lab, to be stored at 4-5°C before further analysis.

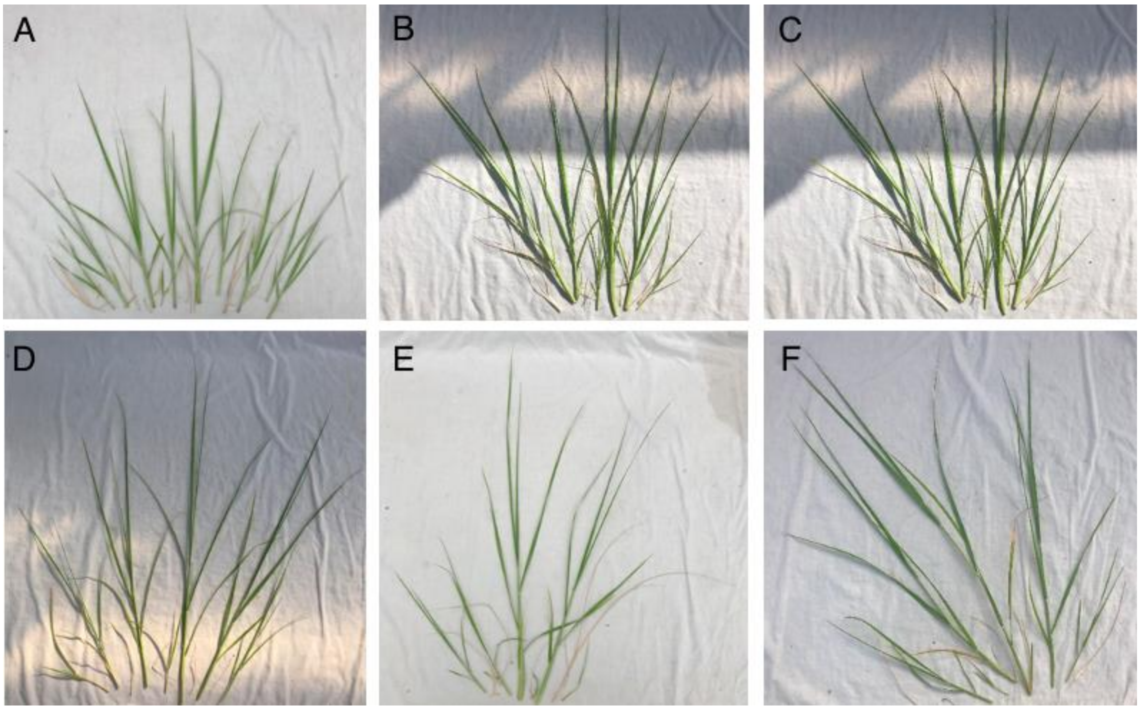

Figure 1 Aboveground biomass of teff genotypes after harvest (A) Addisie, (B) Alba, (C) Balami, (D) Beten, (E) T10, and (F) T11.

2.4 Shoot traits

The height of the teff plants was measured in the green house before harvest and was measured from base to the tip of flag leaf. Moreover, number of tillers were counted in the greenhouse after harvest. Aboveground biomass was determined in the lab for the individual teff samples. The samples were dried at 70°C for 24 h before weighing (Siddique et al., 1990).

2.5 Root analysis and plant biomass allocation

At the lab, root samples were imaged. Three roots per soil depth level were placed individually on a 20 by 20 cm squared petri dish filled with water and scanned. Scans were made on an Epson Expression 10000 XL scanner, and imported to WinRhizo (Regent Instruments Inc., Québec City, Canada; scanner resolution; 400 dpi, grey-scale; automatic thresholding). WinRhizo is a software for analyzing root morphological traits and has been widely used both on teff roots and roots of other grass species such as wheat and oat (Gebrehiwot et al., 2020; Himmelbauer et al., 2004; Nakhforoosh et al., 2021).

After scanning, each of the roots was placed on a smaller petri dish and stored as with the bulk samples, for drying and later weighing. As for the rest of the bulk root mass for the respective depth levels, the number of seminal roots were counted, before, the bulk mass was placed in paper bags and stored for drying and later weighing.

Root data obtained for this study were dry weight (g) of the individually scanned roots and dry matter of the bulk. Root dry weight was determined following the same procedure as with aboveground dry. In addition, root diameter (mm; RDIA), root length (m), and root volume (cm^3) were extracted from WinRhizo. For each plant sample the following traits were calculated: BGBM; R:S; vertical root distribution (β); SRL; RTD; and RDIA (Table 2). The root traits were calculated for each of the three individually scanned roots per depth, and then the average of these was calculated, for further statistical analysis. SRL is the ratio of root length to dry mass of roots, and RTD is the ratio of weight and volume of the root and was calculated according to equations I and II:

I. $$SRL\ m\ g^{-1} = \frac{root\ lenght\ (m)}{root\ dry\ weight\ (g)}$$

II. $$RTD\ g\ cm^{-3} = \frac{root\ dry\ weight\ (g)}{root\ volume\ (cm^3)}$$

Average RDIA was calculated as the average of the individual RDIA of the three scanned roots per depth. R:S is the ratio between belowground root dry mass and aboveground dry mass, and were calculated according to equation III:

III. $$R{:}S = \frac{root\ dry\ weight\ (g)}{shoot\ dry\ weight\ (g)}$$

Calculations of the β, which constitutes a measurement of the shallowness of the root system, are based on the model $Y=1- \beta^d$ proposed by Gale & Grigal, (1987), where Y is the cumulative root fraction, and d the soil depth (cm). Cumulative root fraction is calculated according to equation IV, following the rationality of (Fan et al., 2016):

IV. $$Y_i(d) = \frac{root\ DM_i(d)}{root\ DM_{max-i}}$$

Where $Y_i\,(d)$ is the root mass fraction of a given depth, $root\ DM_i\,(d)$ is root dry matter at the given depth in the soil profile and $root\ DM_{max}$ is the total root dry mass for the soil profile. To calculate the β values, $Y=1-\beta^d$ was used as a fit equation with the 'nls' function (R Core Team, 2021).

Table 2 List of the traits investigated in this study. Height, Tiller and AGBM constitutes the aboveground shoot traits; SR, BGBM, R:S and β constitutes the architectural root traits; SRL, RTD and RDIA constitutes the morphological root traits.

Trait Class	Trait	Unit	Description
Aboveground traits	Height	cm	Height of teff plant measured from base to the tip of flag leaf.
	Tiller	n	Number of tillers per teff plant.
	AGBM	g	Total aboveground biomass.
Architectural traits	SR	n	Number of seminal roots per teff plant.
	BGBM	g	Total belowground biomass.
	R:S		Root to shoot ratio.
	β		Measure of the shallowness of rooting based on the cumulative root fraction.
Morphological traits	SRL	$m\ g^{-1}$	Specific root length, constitutes the root length per unit root weight.
	RTD	$g\ cm^{-3}$	Root tissue density, constitutes root mass per root volume.
	RDIA	mm	Average root diameter.

2.6 Statistics

Data exploration, statistical analysis and, graphical illustrations were conducted by using the statistical coding software R version 4.0.5 (R Core Team, 2021; Wickham, 2016). The data was investigated under consideration of a potential block effect caused by a potential increase in growth due to the time, between harvest of the blocks. In order to investigate the block effect and the independence of the variances, an initial mixed effect model for analyzing the randomized block design was given:

Model 1 → $\mathrm{lm}(Y \sim \mathrm{genotype} * \mathrm{treatment} * \mathrm{depth} * \mathrm{block})$

Model 2 → $\mathrm{lm}(Y \sim \mathrm{genotype} * \mathrm{treatment} * \mathrm{depth} + \mathrm{block})$

The model (model 1) assumes an interaction between the effects of genotype, treatment, depth, and block, on the dependent variable Y, which represents a specific root trait. Model 1 was tested against a corresponding model (model 2), where the effect of block was assumed to be additive rather than multipliable in an analysis of the variances test (ANOVA) on a p = 95 % level. For aboveground traits, and architectural traits, where soil depth was not a parameter, the depth parameter was excluded from the models. In all instances, traits had a $p \geq 0.05$, and the effect of block is assumed to be additive, see supplementary table in the appendix (Table S2). Thus, the effect of block does not interact with the other variables, and the relative difference between the blocks is assumed to be the same and can be excluded from the rest of the statistical analysis.
After investigating the independence of the variances, the data were subjected to the Shapiro-Wilk normality test, see supplementary table in the appendix (Table S3). Certain traits diverted from normal distribution, and this was regulated by transforming the data, either by logarithmic transformation or by squaring the data in order to secure a better fit. Outliers were identified by using the interquartile range and removed. At last, the data was subjected to Levene's test of homogeneity of variances, see supplementary table in appendix (Table S3). All traits but RDIA followed the assumptions (normality, homogeneity, and independence) that the ANOVA requires. To this end, two glm models (model 3; model 4) were formulated and used for further analysis:

Model 3 → $\mathrm{glm}(Y \sim genotype * treatment)$

Model 4 → $\mathrm{glm}(Y \sim genotype * treatment * depth)$

The models underwent ANOVA respectively, testing for the main effects of either genotype, treatment, and depth, as well as testing for 2-way and 3-way interactions. Note that the models do not have the effect of block since this effect was assumed to be additive. Furthermore, the models differ in that the depth parameter is included for model 4, which then exclusively was used for the morphological traits.
For the morphological root traits, SRL and RTD were subjected to regular ANOVA tests, however, RDIA diverted from the assumption of normality, and therefore each main effect was tested individually by the non-parametric Kruskal-Wallis test.

Results of the morphological traits were reported as means across treatments. In order to detect which genotypes differed from each other, a post-hoc analysis, across depth, with Tukey adjustment, from the R package "Agricolae", was used (Mendiburu & Yaseen, 2020). Moreover, a t-test was used to pairwise compare the depths, grouped by genotype. Due to the divergence from normal distribution the nonparametric Duuns test from the R package "FSA" was used for post-hoc analysis of RDIA (Ogle et al., 2021). In turn, Duuns test was used to analyse depth differences for RDIA between the genotypes.

As with the morphological traits, the aboveground traits, and architectural traits, underwent post-hoc analysis with Tukey adjustment to detect differences between the genotypes (Mendiburu & Yaseen, 2020). However, the genotypes were grouped based on the treatment. Thus, the results reflect the mean values of the given traits, and the differences between the genotypes in both treatments, except for vertical root distribution which is reported as the mean across treatments. Moreover, t-test was used on the individual genotypes in order to detect differences between treatments.

At last, spearman's rank correlations, from the R package "Corrplot", was used to identify potential correlations between traits, due to the divergence from normal distribution detected in RDIA (Wei, 2021).

3 Results

3.1 Aboveground traits

From the ANOVA test, a significant effect of differences between genotypes and on treatments was detected for all aboveground traits (Table 3). The lowest and highest tiller numbers were detected in treatment N-, where tiller numbers ranged between 3.5 in Alba to 7.9 in Addisie (Table 4). Under low nitrogen supply, tiller number did not differ between Addisie, T11, and Beten, but reached significantly greater values, compared to Balami, T10 and Alba, which in turn did not differ from each other (Table 4). For treatment N+, tiller number ranged between 3.8 in Alba to 7.8 in Beten (Table 4). Tiller numbers were significantly higher for Beten and Addisie compared to T10 and Alba which in turn did not differ from each other, under high nitrogen supply.

Table 3 Analysis of variances of number of tillers per teff plant (Tiller) teff plant height (Height) and aboveground biomass (AGBM). The aboveground traits were subjected to two-way ANOVA, which included genotype and treatment as independent parameters. ANOVA's were evaluated on a significance level ($p < 0.05$). Parameters with a significant effect are denoted with an asterisk.

Factor	**Effects on traits (*p* value)**		
	Tiller	**Height**	**AGBM**
genotype	4.61e-19 *	2.74e-18 *	4.30e-02 *
treatment	3.10e-02 *	1.60e-02	5.30e-09 *
genotype:treatment	4.50e-02 *	1.33e-01	3.26e-01

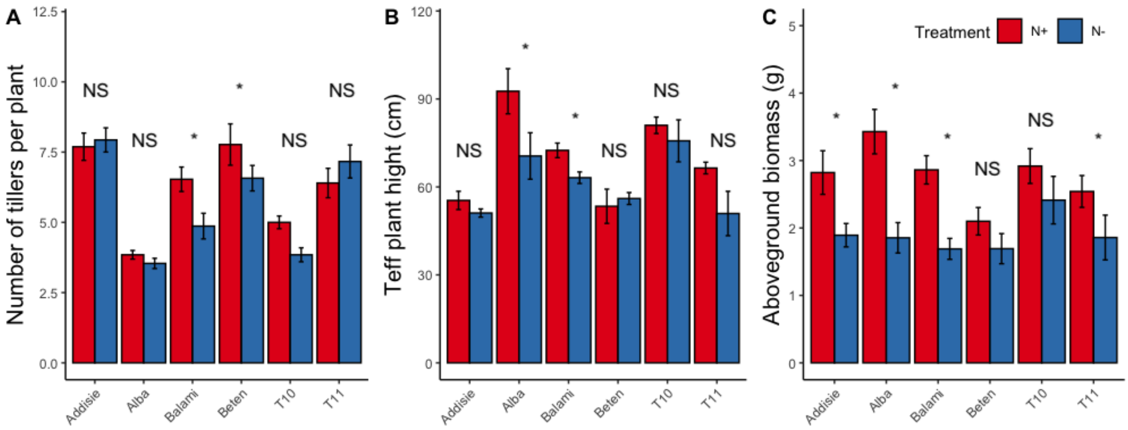

Figure 2 Number of tillers per plant (A), plant height (B) and accumulated aboveground biomass (C) of six *Eragrostis tef* genotypes growing at two nitrogen regimes, i.e., high N+ and low N- treatments; see text for details. Asterisk's indicate significant differences between treatments (t-test; $p < 0.05$; $n = 12 - 15$; mean±SE); NS = not significant.

Tabel 4 Mean values of the aboveground traits of six teff genotypes; plant shoot height (Height), tillers per plant (Tillers) and total aboveground biomass, per plant (AGBM). Different letters indicate significant differences between genotypes' traits at the given treatments (N+ and N-). Values are reported as mean ± SE (Tukey test, n = 12 - 15, $p < 0.05$).

Treatment	Genotype	Tiller numbers	Height (cm)	AGBM (g)
N+	Addisie	7.7 ± 0.44^{a}	52.6 ± 1.67^{e}	2.82 ± 0.32^{ab}
	Alba	3.8 ± 0.15c	97.1 ± 3.9^{a}	3.43 ± 0.33^{a}
	Balami	6.5 ± 0.43^{ab}	72.4 ± 2.5^{bc}	2.86 ± 0.21^{ab}
	Beten	7.8 ± 0.74^{a}	60.4 ± 1.7^{de}	2.10 ± 0.20^{b}
	T10	5.0 ± 0.23^{bc}	81.0 ± 2.8^{b}	2.92 ± 0.26^{ab}
	T11	6.4 ± 0.52^{ab}	66.4 ± 2.0^{cd}	2.54 ± 0.24^{ab}
N-	Addisie	7.9 ± 0.43^{a}	51.1 ± 1.4^{c}	1.89 ± 0.17^{a}
	Alba	3.5 ± 0.18^{b}	81.4 ± 3.3^{a}	1.85 ± 0.23^{a}
	Balami	4.9 ± 0.45^{b}	63.1 ± 2.0^{b}	1.69 ± 0.16^{a}
	Beten	6.6 ± 0.45^{a}	56.0 ± 2.0^{bc}	1.69 ± 0.22^{a}
	T10	3.8 ± 0.25^{b}	78.0 ± 4.2^{a}	2.41 ± 0.35^{a}
	T11	7.2 ± 0.59^{a}	60.3 ± 2.7^{bc}	1.85 ± 0.33^{a}

Balami and Beten showed significantly higher numbers of tillers under high nitrogen levels; Balamis' tiller numbers increased by 32.6 %, and Betens' by18.2 % (Table 4; Figure 2A). For the other genotypes, no significant differences were detected between treatments, however, Alba and T10 tended to follow the pattern of Balami and Beten, with higher tiller numbers under N+ treatments.

The high nitrogen treatment N+ produced the tallest plants. Teff height ranged between 52.6 cm in Addisie, to 97.1 cm in Alba (Table 4). Alba was the significant tallest among genotypes, and Addisie the lowest genotype, differing significantly from all but Beten (Table 4). Variations between genotypes in treatment N- were less scattered, however still significant between certain groups. Alba and T11 achieved the tallest mean height and differed significantly from all other genotypes. On the other hand, Addisie achieved the lowest height, but did not differ significantly from Beten and T11 (Table 4). Differences between the treatments on the individual genotypes occurred for Alba (+14.7%) and Balami (+19.2%) which both showed significant effects when fertilized with N+ (Table 4; Figure 2B).

The largest AGBM accumulation per plant was found in fertilized treatments N+, ranging between 2.1 g in Beten to 3.4 g in Alba (Table 4). At N- conditions, AGBM accumulation ranged from 1.7 g in Balami and Beten, to 2.4 g in T10 (Table 4). Variations of accumulated AGBM between genotypes were scarce. Under N+ significant differences occurred between Alba and Beten, which in turn did not differ significantly from any of the other genotypes (Table 4). In treatment N-, AGBM differences were not significant (Table 4). Significant differences between treatments were detected for genotypes Addisie, Alba, Balami, and T11 which all possessed an increased AGBM under high nitrogen supply.

3.2 Root architectural traits

Significant effects of fertilisation were detected for all traits but for the regression coefficient β (Table 5). Differences between genotypes were detected in the traits R:S ratio and the regression coefficient β (Table 5).

The highest numbers of SR were detected for plants in treatment N+, where SR ranged from ~26 in T11 to ~29 in Addisie (Table 6). Lowest SR numbers were found in treatment N- where SR ranged from 21 in T11 to ~27 in T10. No significant differences were detected between the genotypes. That said, the effect of treatment on SR number between the individual genotypes was significant. The number of SR increased significantly in genotypes Addisie, Balami and T11 under high nitrogen supply by 23.7 %, 15.6 % and 24.8 %, respectively (Table 5; Figure 3A).

Table 5 Analysis of variances of belowground biomass (BGBM), root to shoot ratio (R:S) number of seminal roots per teff plant (SR) and the beta value (β). The architectural root traits were subjected to two-way ANOVA, which included genotype and treatment as independent parameters. ANOVA's were evaluated on a significance level ($p < 0.05$). Parameters with a significant effect are denoted by an asterisk.

Factor	**Effects on traits (*p* value)**			
	BGBM	**R:S**	**SR**	**β**
genotype	7.30e-02	1.94e-08 *	1.81e-01	5.40e-15 *
treatment	9.08e-07 *	2.00e-03 *	1.33e-05 *	1.78e-01
genotype:treatment	5.68e-01	7.92e-01	7.12e-01	4.77e-01

In regard to BGMB values, no significant differences between the genotypes were found in either of the treatments (Table 6). That said, the highest accumulated BGBM was found under N+, whereas mean BGBM ranged between 2.06 g in T10 and 2.38 g in Addisie (Table 6). Mean BGBM values ranged between 1.65 g in Beten to 1.96 g in Addisie for N- treatment (Table 6). Significant differences between treatments were detected, i.e., Alba and Balmi showed remarkable increases in BGBM values under N+ by 52.3 % and 41.7 %, respectively (Table 6; Figure 3B).

Tabel 6 Mean values of the architectural root traits of teff; seminal roots (SR), belowground biomass (BGBM) and root to shoot ratio (R:S). Different letters indicate significant differences between genotypes, at a given treatment (N+ or N-). Values are reported as mean ± SE (Tukey test, n = 12 - 15, p < 0.05).

Treatment	Genotype	SR	BGBM (g)	R:S
	Alba	28.77 ± 1.66[a]	2.56 ± 0.19[a]	0.78 ± 0.046[bc]
	Addisie	29.36 ± 1.23[a]	2.38 ± 0.16[a]	1.00 ± 0.062[ab]
N+	Balami	28.80 ± 1.13[a]	2.72 ± 0.20[a]	0.97 ± 0.056[ab]
	Beten	26.92 ± 1.57[a]	2.08 ± 0.20[a]	1.01 ± 0.048[a]
	T10	27.84 ± 1.24[a]	2.06 ± 0.16[a]	0.70 ± 0.041[c]
	T11	26.20 ± 1.12[a]	2.10 ± 0.12[a]	0.89 ± 0.055[abc]
	Addisie	23.73 ± 1.05[a]	1.96 ± 0.13[a]	1.05 ± 0.052[ab]
	Alba	24.62 ± 1.49[a]	1.68 ± 0.20[a]	0.92 ± 0.036[bc]
N-	Balami	24.93 ± 1.17[a]	1.92 ± 0.21[a]	1.15 ± 0.057[a]
	Beten	24.13 ± 2.01[a]	1.65 ± 0.21[a]	1.03 ± 0.055[abc]
	T10	26.61 ± 1.88[a]	1.76 ± 0.15[a]	0.82 ± 0.063[c]
	T11	21.00 ± 1.96[a]	1.74 ± 0.24[a]	0.94 ± 0.065[abc]

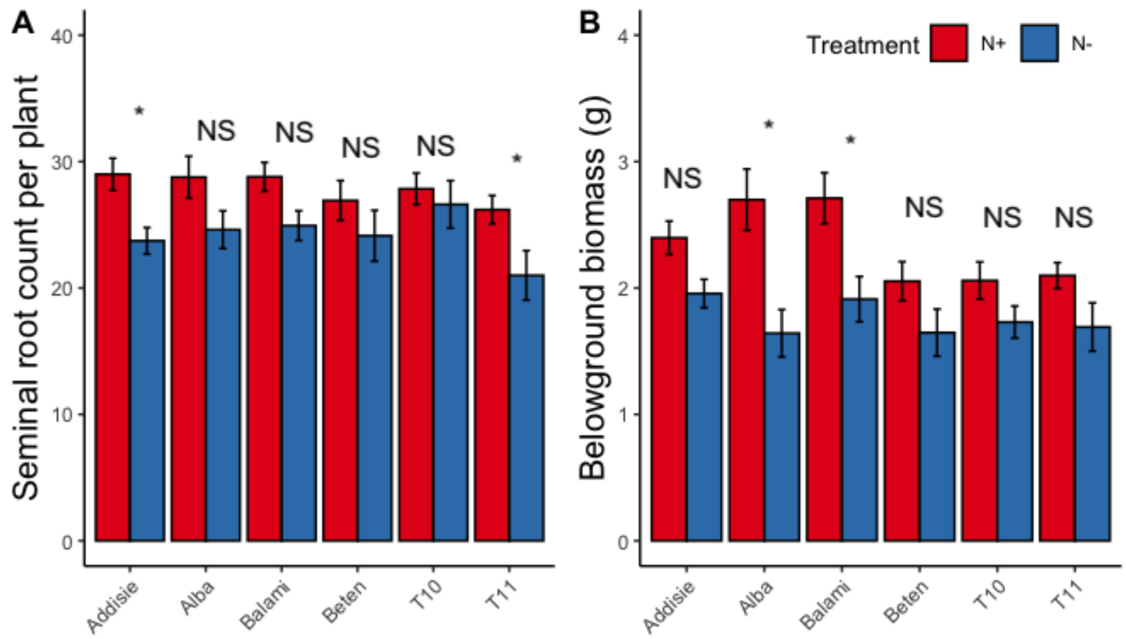

Figure 3 Mean values of architectural traits seminal roots per plant (A) and belowground biomass (B) between the teff genotypes under two nitrogen fertilisation regimes (N+ and N-). Asterisk's indicate significant differences between treatments (t-test; $p < 0.05$; n = 12 - 15, mean±SE); NS = not significant.

Root shoot ratio was affected significantly by treatment, and according to genotype. Variations of mean R:S were significant between multiple genotypes in N-, and ranged between 0.82 in T10 to 1.15 Balami (Table 6). Contrasts were not significant between Balami and T10, and between Beten and T11, and the rest of the genotypes (Table 6). At treatment N+, R:S ranged between 0.78 in Alba to 1.00 in Beten (Table 6). Here multiple genotypes differed significantly from each other, however, differences between Beten Balami and Addisie were not significant (Table 6). Addisie and Balami did not differ significantly from Alba which in turn did not differ significantly from T10 with the lowest R:S values. T11 did not contrast any of the genotypes (Table 6). Significant increases in R:S were detected in Alba (17.7 %) and in Balami (18.5 %) when treated with N- (Figure 4).

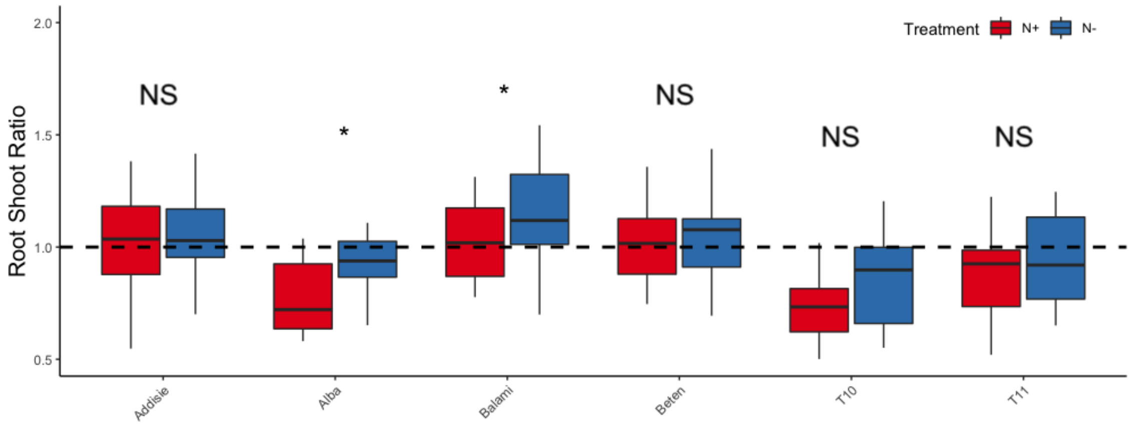

Figure 4 Boxplot representing mean values of root shoot ratio of teff genotypes under two nitrogen regimes (N+ and N-). The dashed line represents a balanced allocation to aboveground and belowground biomass. Asterisk's indicate significant difference between treatments (t-test; $p < 0.05$, n = 12 - 15, mean±SE).

The vertical root distribution coefficient, the β value, was not affected by treatment, but exclusively differed between genotypes (Table 5). To this end, results of the vertical root distribution will here be reported as the mean across treatments. β values ranged between 0.963 in Alba to 0.972 in Beten (Figure 5). With the highest β value, Beten differed significantly from Addisie, T11, T10, and Alba. Differences between Betens' and Balamis' β of 0.972 and 0.970 were not significant (Figure 5). A common feature for all genotypes was that the top 50 % of the root biomass was allocated in the top 0-30 cm of the soil column (Figure 5).

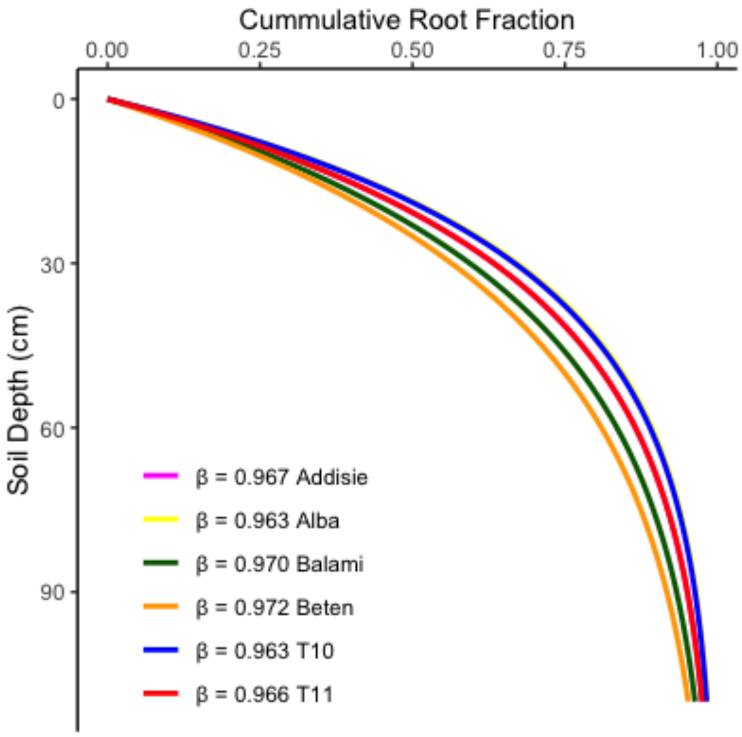

Figure 5 Vertical root distribution of the cumulative root fraction on depth of six teff genotypes growing in large soil columns. Cumulative root fraction represents the root mass in percentage from the top 0 cm of the soil column and down. Cumulative root fraction was plotted against depth, and the regression coefficient β, represent a measure of the shallowness of the root system, was determined by fitting the equation $Y=1-\beta^d$.

3.3 Morphological root traits

The morphological root traits were tested for effects of the treatments, and between genotypes, as it was with the aboveground traits and architectural root traits. However, a third parameter was considered, namely the differences between depth levels through the soil column (Table 7). No significant effect of treatment was found for either SRL, RTD, or RDIA, therefore values of the morphological root traits is reported across treatments (Table 8). For detailed data on root trait values in the different treatments, and on different depth levels for all genotypes see Table S4 in the appendix. Mean values of SRL ranged from ~344 m g^{-1} in Beten to ~421 m g^{-1} in T11 (Table 8). T11 had significantly higher SRL values than Beten (344 m g^{-1}), Balami (370 m g^{-1}) and Addisie (379 m g^{-1}), however, did not differ significantly from T10 (409 m g^{-1}) or Alba (397 m g^{-1}).

Table 7 Analysis of variances of specific root length (SRL), root tissue density (RTD) and root diameter (RDIA) of six teff genotypes growing under N+ and N- conditions in large soil columns; see text for details. SRL and RTD were subjected to three-way ANOVA, which included genotype, treatment and depth as independent parameters. Due to the departure from normal distribution RDIA was subjected to Kruskal Wallis non-parametric analysis of variances on each of the main effects. ANOVA's were evaluated on a significance level of $p < 0.05$. Parameters with a significant effect from the independent variable are denoted with an asterisk.

Factor	Effects on traits (*p* value)		
	SRL	**RTD**	**RDIA§**
genotype	5.27e-09 *	6.00e-03 *	1.02e-02 *
treatment	1.68e-01	5.20e-02	1.36e-01
depth	8.31e-17 *	2.23e-04 *	2.56e-03 *
genotype:treatment	6.80e-02	8.63e-01	–
genotype:depth	2.88e-01	9.50e-02	–
treatment:depth	3.58e-01	8.39e-01	–
genotype:treatment:depth	9.00e-01	7.64e-01	–

§Due to the departure from normal distribution, RDIA was subjected to Kruskal Wallis non-parametric analysis of variances on each of the main effects.

Table 8 Morphological root traits of six teff genotypes; specific root length (SRL), root tissue density (RTD) and root diameter (RDIA). Treatments and depths were combined for analysis; no significant treatment effects were found; see Fig. 6 for changes with depth. Different letters indicate significant differences between genotypes per trait. Due to the departure from normal distribution RDIA was subjected to the nonparametric Duuns test. Values are reported as mean ± SE (Tukey test and Duuns test, $p < 0.05$, n = 12 - 15).

Genotype	SRL ($m\ g^{-1}$)	RTD ($g\ cm^{-3}$)	RDIA (mm)§
Addisie	379.20 ± 7.59^{bc}	$0.0855 \pm .0018^{a}$	$0.204 \pm .0024^{b}$
Alba	396.74 ± 9.49^{abc}	$0.0799 \pm .0020^{ab}$	$0.206 \pm .0029^{b}$
Balami	370.37 ± 9.47^{cd}	$0.0766 \pm .0020^{b}$	$0.221 \pm .0030^{a}$
Beten	343.88 ± 6.56^{d}	$0.0824 \pm .0021^{ab}$	$0.218 \pm .0027^{a}$
T10	409.09 ± 9.60^{ab}	$0.0799 \pm .0020^{ab}$	$0.206 \pm .0029^{b}$
T11	421.08 ± 11.01^{a}	$0.0797 \pm .0019^{ab}$	$0.205 \pm .0032^{b}$

§Due to the departure from normal distribution, RDIA was subjected to the nonparametric Duuns test.

Alba and T10 did not differ significantly from Addisie, and Beten had significantly lower values than all the other genotypes but Balami (Table 8). Mean values of the RTD ranged between 0.077 g cm^{-3} in Balami to 0.086 g cm^{-3} in Addisie (Table 8). Balami and Addisie differed significantly from each other, however, not from any other genotype (Table 8).

The highest mean values of RDIA were found in Balami (0.221 mm) and Beten (0.218 mm) and they contrasted RDIA values, found in the rest of the genotypes, ranging from 0.204 mm in Addisie, to 0.206 in both T10 and Alba (Table 8).

Mean values of morphological root traits were indeed different between depth levels through the soil column. Between the genotypes, the general variation of SRL values through the revealed a pattern of lower values at the top layers, and then as the soil depth decreases, SRL in turn increases (Figure 6A). The lowest values of SRL were found at a soil depth of 0-20 cm, with a mean of 317 m g^{-1}. SRL increased significantly at depth level 20-40 cm (409 m g^{-1}). However, the SRL mean at 40-60 cm (423.1 m g^{-1}) and below 60 cm (396.1 m g^{-1}) were similar to values at depth level 20-40 (Figure 6A). Slight differences between the genotypes were detected at several depth levels. Differences in mean SRL between genotypes at soil layer 0-20 cm were not significant (Figure 6A). At depth level 20-40 cm, Beten had significantly lower SRL values than T10, and at depth level 40-60 cm to > 60 cm Beten significantly differed from Alba, T10 and T11 (Figure 6A).

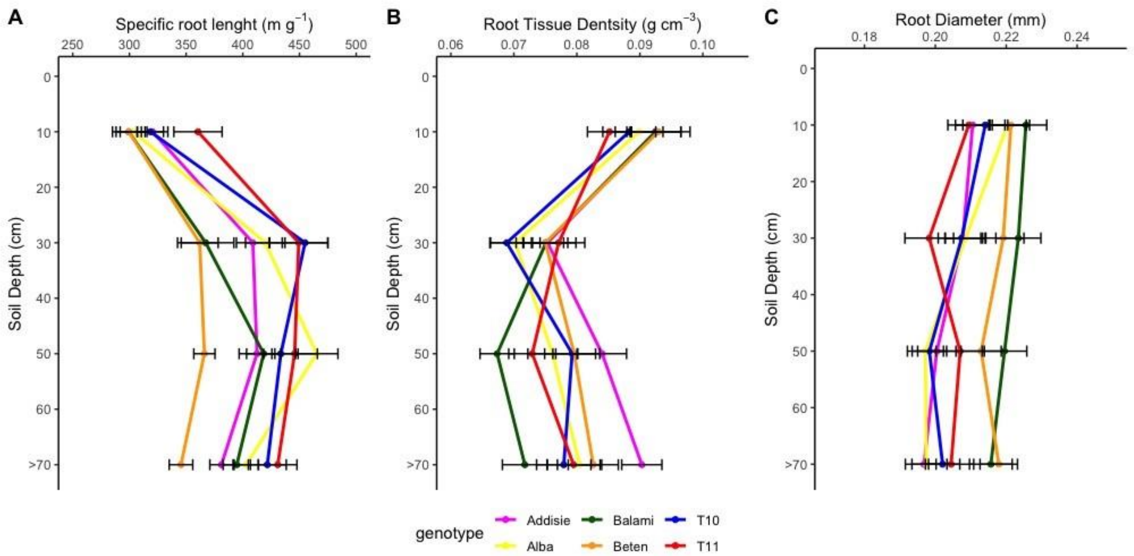

Figure 6 Mean values of (A) specific root length (m g^{-1}), (B) root tissue density (g cm^{-3}) and (C) root diameter (mm) of six teff genotypes, plotted against soil depth; sampling occurred at depth intervals of 20 cm. Horizontal bars signify standard error of the means. For detailed data on root trait values in the different treatments, and on different depth levels for all genotypes see appendix (Table S4).

Contrary to the SRL depth pattern, RTD revealed a pattern of higher mean RTD values in the uppermost soil layers, and then with decreasing depth, RTD in turn decreases

(Figure 6B). The highest mean values of RTD were found at soil depth layer 0-20 cm with 0.09 g cm^{-3}. At depth level 20-40 cm mean RTD decreased significantly to 0.074 g cm^{-3} (Figure 6B). Differences of RTD between genotypes at 20-40 cm and 40-60 cm were not significant, as were differences between 40-60 cm and > 60 cm (Figure 6B). That said, the slight increase between depth layers 20-40 cm and > 60 cm, were in fact significant, however the RTD at depth layer > 60 cm was still significantly less than at the uppermost 0-20 cm (Figure 6B).

As depicted in Figure 6C, the RDIA changed slightly throughout the soil column. The largest values of mean RDIA were found on the uppermost 0-20 cm with a mean of 0.217 mm; RDIA decreases with decreasing depth. No significant differences were detected between 0-20 cm 40-60 cm. However, RDIA were detected to be significantly smaller at > 60 cm as opposed to the top layer (0-20 cm). Differences in RDIA between genotypes were not significant in different soil depth levels (Figure 6C).

3.4 Correlations between traits

Among aboveground traits, several correlations were found. Plant height correlated negatively with tiller number (r = -0.44) and positively with AGBM (r = 0.64) at level ($p<0.05$) (Figure 7). Between the architectural traits, a strong positive correlation was found between SR and BGBM (r = 0.72), and a moderate negative correlation between SR and R:S (r = -0.3). The β coefficient was independent of all architectural traits except a positive correlation with R:S (r = 0.38). Among the morphological root traits, a negative correlation was found between SRL and RDIA (r = -0.55 and between RDIA and RTD (r = -0.52) (Figure 7). Correlations between aboveground traits and root architectural traits were also detected; strong positive correlations were detected between AGBM and SR (r = 0.73) and between AGBM and BGBM (r = 0.80), and a strong negative correlation was detected between AGBM and R:S (r = -0.62) (Figure 7).

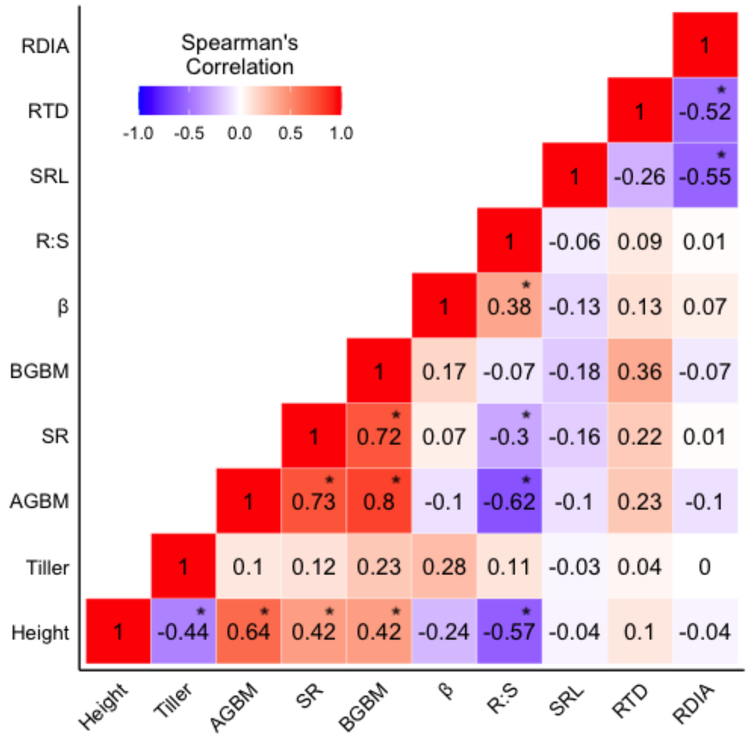

Figure 7 Pairwise Spearman correlation matrix of aboveground traits, Height, number of tillers and (AGBM), architectural root traits, SR, BGBM, β and R:S, and morphological root traits SRL, RTD and RDIA, of six teff genotypes growing under N+ and N- conditions; see text for details. The scale ranges from -1, 0 to 1, with a gradual shift from violet to red indicating r^2 values; significant correlations are denoted with an * (Spearman's rank correlations; $p < 0.05$); for p values check the appendix (Table S5).

4 Discussion

4.1 Characterization of teff traits

Number of tillers per plant varied substantially between genotypes and ranged between 3.5 and 7.9 tillers per plant. Addisie, Beten, and T11 produced most tillers, Alba produced the least number of tillers and T10 was intermediate. Previous studies on teff report contrasting numbers of tillers. A growth chamber study by Plaza-Wüthrich et al., (2013) who investigated certain aboveground agronomic traits of 20 genotypes including Addisie, Alba, Balami, and Beten, reported between 0 and 3.4 tillers per plant, excluding the main stem. This is considerably lower than what was observed among samples in this study. That said, Plaza-Wüthrich et al., (2013), harvested at maturity, and there is no mentioning whether non-productive tillers were excluded, whereas, in the results reported here, all tillers were included. On the other hand, Bayable et al., (2020) reported a mean of 8.57 tillers per plant among several teff genotypes (both landraces and improved varieties)—which resembles the results determined here.

While Alba showed the fewest tillers, it was in fact the tallest among the genotypes. On the other hand, Addisie which produced an abundant number of tillers was among the shortest genotypes. This suggests an inverse relationship between the two traits, which is confirmed by the clear negative correlation ($r = -0.44$, $p < 0.05$). Another study on teff by Mengie et al., (2021) did not find any correlation between height and number of tillers; however, the inverse relationships between plant height and the production of tillers have been confirmed in previous studies on rice (Oryza sativa) and wheat (Triticum sp.) (Liao et al., 2019; Sharma, 1995).

The aboveground biomass (AGBM) was affected by nitrogen fertilisation levels. In terms of numbers of tillers, Beten and Balami significantly increased tiller production by 32.6 % and 18.2 %, respectively, under additional N+ fertilisation.

A significant increase in plant height of 19.2 % and 14.7 % were detected for Alba and Balami respectively, under high nitrogen supply. Although only a few genotypes were affected by treatment in respect to tillers and plant height, the effect of treatment becomes rather clear when looking at total AGBM. For AGBM, Addisie, Alba, Balami, and T11 showed significantly higher values on N+ treatments as opposed to N- treatments. In this study, only tiller number and height were included while many other shoot traits are known to influence AGBM such as area and amount of leaves per plant (Figueroa-Bustos et al., 2018; Rai et al., 2018). That said increase AGBM in this study can largely be ascribed to an increase in plant height rather than tiller production due to the positive correlation between height and AGBM ($r = 0.64$, $p < 0.05$), and the previously mentioned inverse relationship between height and tiller numbers.

Root shoot ratio (R:S) of the teff genotypes ranged between 0.70 to 1.15. Differences were significant between genotypes Balami, Addisie, and Beten which possessed highest R:S, as opposed to Alba and T10 in the low end, and T11 with an intermediate R:S ratio. The R:S reported in this study are substantially larger than for crops such as wheat and millet (Setaria italica) (Nadeem et al., 2018; Tolley & Mohammadi, 2020). High R:S is regarded as a desired ideotype root trait in breeding programs aimed towards drought-tolerant crops, which could indicate a connection between drought tolerance and root traits of certain teff genotypes (Govindaraj et al., 2010; Karcher et al., 2008). That said, a microbiological study on growth-promoting rhizobacteria, reported R:S values of teff, ranging between 0.23 and 0.34 (Woyessa & Assefa, 2011). Whereas teff in the present study was harvested at the vegetative stage at 51 DAS, Woyessa & Assefa, (2011) harvested at maturity at 75 DAS which could have contributed to more aboveground growth, thereby lowering R:S values.

R:S constitutes the relationship between total aboveground and belowground biomass (BGBM), that said, there was no significant correlation between R:S and BGBM. Compared to mature stage wheat plants, which exhibit BGBM values between 5.28 g and 8.37 g, BGBM of teff plants reported in this study was quite low ranging between 1.65 g to 2.72 g (Ehdaie et al., 2011). Not surprisingly though, BGBM were strongly correlated with seminal root number (SR) ($r = 0.72$, $p < 0.05$). With SR numbers ranging between 21-29 per plant, Teff exhibited a high degree of SR growth compared to wheat where two different studies reported SR numbers between 3 to 8, and 4 to 6 (Fernando et al., 2020; Xu et al., 2021).

For vertical root distribution, β values ranged between 0.963 to 0.972 which is substantially higher than β values reported in other grass species such as perennial ryegrass (Lolium perenne) with an β between 0.89 to 0.92 and wheat with a β between 0.84 to 0.95 (Dirks et al., 2021; Streit et al., 2019). The high beta values for teff suggest steep and deep-reaching roots, rather than, a shallow root system with high lateral branching. A steep and deep root system has been suggested as an ideotype trait for breeding towards drought tolerance properties in maize—possessing beta values similar to those of teff (Grieder et al., 2013; Neykova et al., 2011).

Values of the morphological root traits of teff varied significantly between genotypes but were not affected by nitrogen level. Greatest variations were found in specific root length (SRL) which exhibited values ranging between 343.88 m g-1 and 421.08 m g-1. These SRL values were rather high compared to other grass crops such as those found in wheat and oat (Løes & Gahoonia, 2004; Wendling et al., 2016). On the other hand, root diameter (RDIA) values were comparable to RDIA of those found in wheat and oat, whereas RTD values for teff were considerably higher (Løes & Gahoonia, 2004; Wendling et al., 2016). Since SRL is, the root length per unit of dry weight, and RTD is the unit of dry weight per unit volume, high SRL should in theory yield lower RTD and RDIA values (Ryser & Lambers, 1995). It was not the case in this study where no correlation was detected between SRL and RTD. The relationship between SRL, RTD, and RDIA observed in this study, mirrors that found in several species of perennial grasses where no correlation between RTD and SRL was found (Picon-Cochard et al., 2012).
The teff genotypes exhibited a general pattern of relatively low SRL values in the top 0-20 cm soil layer, where after SRL gradually increased by depth. Contrary to the SRL depth pattern, RTD values exhibited greater values in the top 0-20 cm with a gradual decrease by depth. Where substantial changes according to depth level were observed for SRL and RTD, RDIA values look rather homogenous, however with slightly higher values in shallower soil layers. The general pattern of the morphological root traits of teff reported here are in line with patterns observed in previous studies on wheat, which confirms the tendency of higher values of SRL and RDIA contrary to lower RTD values in shallow soil layers (Mehrabi et al., 2021; Peng et al., 2019). The high SRL values reported in this study suggest great exploration capabilities of teff which could be connected to the drought tolerance otherwise exhibited by teff (Cheng et al., 2017). Sun et al., (2013) found a connection between high SRL in the top 20 cm soil layer and drought tolerance of tall fescue (Festuca arundinacea). Tsuji et al., 2005) found that sorghum (Sorghum bicolor) exhibited higher SRL when subjected to a dry environment as opposed

to wet environments; however, since teff plants in the present study were rather well irrigated and further research would be needed to confirm this connection.

4.2 Effect of altered nitrogen availability on teff root system properties

Effect of N fertilization was detected for all architectural root traits except vertical root distribution. There were no significant differences between the genotypes on either treatment, for SR and BGBM. That said, differences in SR and BGBM values were detected between treatments for certain genotypes. SR values of Addisie and T11 increased significantly on the N+ treatment relative to the N- treatment. Moreover, Alba and Balami significantly increased BGBM when subjected to N+ treatments. These results paint a picture of little variations between the treatments and thus a little effect of nitrogen level, however with a tendency for greater root biomass and SR with greater nitrogen availability. The results reported here are in line with those of Dong et al., (2018) who observed higher SR numbers with higher NO3- concentration in rice (Oryza sativa). In contrast Wang et al., (2020) observed that nitrogen-limited rice plants would increase the number of SR which indicates that within grass crops response to nitrogen level differs even within genotype as shown for teff in the present study.

The BGBM results presented here reflect other studies on genotypes of wheat and maize (Zea) and certain grass forage species, which reports no decrease in BGBM with decreased nitrogen level (Skinner & Comas, 2010; Shangguan et al., 2004; Y. Wang et al., 2004).

Vertical root distribution was unaffected by treatment. This contrasts with the results from a similar greenhouse study where grasses subjected to low nitrogen environments tended to expand their root systems relative to the controls (Skinner & Comas, 2010). All though Skinner & Comas, (2010) found a tendency of greater variation of vertical root distribution when plants were subjected to low N, they emphasize that only a small proportion of species showed significant differences and conclude that other parameters such as drought has greater effect on root distribution.

Where BGBM and SR exhibited increased values under N+ treatments, R:S was generally lower under on N+ treatments relative to N- treatments. For Alba and Balami R:S were significantly affected by the nitrogen treatments 17.9 % and 18.5 % larger R:S, on N-treatments. Larger R:S in nitrogen-poor environments have in turn been observed for several wheat varieties (Li et al., 2009; Shangguan et al., 2004).

4.3 Correlation within and between Root and Shoot traits

Teff plant height and AGBM was positively correlated with several architectural root traits; height and SR ($r = 0.42$, $p < 0.05$); AGBM and SR ($r = 0.73$, $p < 0.05$); AGBM and BGBM ($r = 0.8$, $p < 0.05$); Height and BGBM ($r = 0.42$, $p < 0.05$). The general relationship between roots and shoots of teff plants in this study is characterized by a tendency of greater partitioning of assimilates for aboveground biomass contra belowground biomass. As accounted for above, no significant differences were detected between genotypes for SR and BGBM on either of the nitrogen treatments, suggesting a rather rigid behaviour of teff genotypes roots in response to altered nutrients level. On the other hand, variation between the shoot traits, tillers, height and, AGBM was detected which indicates greater plasticity of aboveground traits contra architectural root traits, in relation to nitrogen availability. This is further underlined by the negative correlation between AGBM and R:S ($r = -0.62$, $p < 0.05$) and all though SR showed a week negative correlation with R:S ($r = -0.3$, $p < 0.05$), no significant correlation between BGBM and R:S was detected.

Root morphology was not affected by nitrogen and seemed to be independent of both aboveground traits, and architectural root growth as no correlations was detected. This contrasts other studies that investigated root shoot relations in wheat. Figueroa-Bustos et al., (2018), found strong negative correlations between SRL and BGBM, SRL and RS. Moreover, Figueroa-Bustos et al., (2018) found strong positive correlations between SRL and height, and SRL and AGBM. Corneo et al., (2017) demonstrated how SRL had significant impact on both grain yield, and nitrogen content of leaves, in several wheat accessions. Although morphological traits did not correlate with either architectural or aboveground traits, this study confirms the multidimensionality of morphological root growth with RDIA correlating negatively with both SRL and RTD, ($r = -0.55$, $p < 0.05$) and ($r = -0.56$, $p < 0.05$) respectively (Bardgett et al., 2014; Kramer-Walter et al., 2016; Zhou et al., 2018). Morphological root traits in this study seemed rather rigid in terms of response to the nitrogen levels and lack of correlations with architectural and aboveground traits which is surprising since it could be expected that the high SRL potentially could have increased nitrogen uptake and thus biomass accumulation in N+ treatments. However, Poorter & Ryser, (2015) argue that SRL responds positively in overall nutrient poor environments with localized patches of available nitrogen which also is confirmed by Hodge, (2003). In contrast, nitrogen availability in this study was altered, however the mobile nature of the applied nitrogen could have made the distribution of nitrogen in the soil column rather uniform which in turn could have influenced the morphological root responses.

4.4 Conclusion

This study has provided a comprehensive characterization of architectural and morphological root traits of six genotypes of Eragrostis tef cultivated under low and high nitrogen availability. Of the architectural root traits, seminal roots, and belowground biomass, responded with higher values under high nitrogen supply for certain genotypes, however, vertical root distribution was unaffected of the altered nitrogen conditions. In turn, no effect from the altered nitrogen supply was detected for the morphological root traits. That said, variations between genotypes were detected for vertical root distribution, specific root length, root tissue density and root diameter. The results provided her, suggest greater plasticity of genotypes in respect to aboveground traits in contrast to the rigid root growth under altered nitrogen conditions, and root shoot relations were characterized by greater partitioning of assimilates for aboveground biomass contra belowground biomass. Of the shoot traits investigated here, plant height proved to be the main contributor to increased aboveground biomass. This study will provide needed literature on architectural and morphological root traits and their relationship with aboveground traits of teff and will assist investigations in further elucidating how teff roots impact aboveground agronomic traits.

Acknowledgements

I would like to first give a big thank you to may master thesis adviser Assoc. Prof. Dr. Boris Rewald from Universität für Bodenkultur Wien, for giving me the opportunity to work with teff plants. It was a great pleasure for me to be a part of this project and I truly enjoyed planning and working with the teff plants in the greenhouse in Tulln. You have been a terrific advisor and showed great engagement in the making of this thesis. Thank you for always answering when I had troubles, and for guiding me in the right direction, giving encouragement and inspiration.

I would also like to extend my gratitude's to Senior Researcher Niels Holst from Aarhus University, for your guidance in the statistical work, and for helping me with managing R.

To my colleagues Alissa Holleis, Constantin Müller and Hanna Mayrhofer—you have been essential in getting the results which made this thesis possible. Thank you for your technical assistance with the preparations in the greenhouse, and for helping me manage the teff plants. Thank you for helping with the harvest and for the long days you spend in the lab, scanning 18.37 kilometers of teff roots.

The project was partially supported by the EPPN2020 project "Characterization of the early-stage root architecture and morphology of 25 tef genotypes from contrasting agro-climatic zones in Ethiopia – and their response to nutrient availability (TEF-ROOT)". Rong Chen, Lukas Lorenz and Dr. Marcia R. Gomes de Varvalho's (UTAD, Portugal) help was key to identify contrasting root phenotypes by screening seedlings of 25 teff genotypes at the 2D-RSAT platform (Nottingham, UK) with local support by Dr. Darren Wells and Dr. Jonathan Atkinson. The U.S. National Plant Germplasm System (USDA NPGS) is kindly acknowledged for providing the seeds for this study (order # 32648).

To my colleague and dear friend Thomas Linding Jensen thank you for helping me proofreading several sections of this thesis, I owe you a "larger".

At last, a big thanks to my parents for your support and patience through this process, and for your apparent interest in teff roots in talks on the phone and over the dinner table.

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Appendix

Table S1 Fertilizer recipes for 75 % diluted Hoagland solutions N+ and N-. For N-, KNO_3 were diluted to 10 %; $NH_4H_2PO_4$ and $Ca(NO_3)_2$ were substituted with, KCl and KH_2PO_4 to balance potassium and phosphorus; and $(CaSO_4)$ H_2O_2 was added to balance calcium.

N+					
Name of compound	**Chem. formula**	**Desired concentration**		**g/L**	**For 25 L(g)**
Ammonium Phosphate monobasic	(NH4)3PO4	252,1176	µM	0,029001088	0,725
Calcium Nitrate tetrahydrate	Ca(NO3)2·4H2O	698,7084	µM	0,164999989	4,125
Potassium Nitrate	KNO3	1,5034	mM	0,15199374	3,8
Magnesium Sulphate	MgSO4	1,0219	mM	0,123006103	3,075
Boric Acid	H3BO3	459,9486	µM	0,028440002	0,711
Copper(II) sulphate pentahydrate	CuSO4·5H2O	3,0038	µM	0,000750019	0,019
Manganese Chloride	MnCl2	63,0525	µM	0,007934527	0,198
Molybdenum(VI)oxide	MoO3	1,3895	µM	0,000200005	0,005
Zinc Sulphate heptahydrate	ZnSO4·7H2O	7,9978	µM	0,002300007	0,058
Fe-EDTA		35	µM	0,0147385	0,368
N-					
Name of compound	**Chem. formula**	**Desired concentration**		**g/L**	**For 25 L(g)**
Potassium phosphate monobasic	KH2PO4	251,8186	µM	0,034269993	0,857
Calcium sulphate dihydrate	CaSO4·2 H2O	696,9377	µM	0,119991764	2,999
Potassium Nitrate	KNO3	0,15034	mM	0,015199374	0,379
Potassium Chloride	KCl	0,50064	mM	0,03727718	0,933

Table ANOVA applied on model 1 and model 2 of; aboveground traits, height, number of tillers AGBM; architectural traits, SR, β, R:S and BGBM; and morphological traits, SRL, RTD and RDIA, of the teff genotypes. Degrees of freedom (DF) for each model is reported, along with the distribution ratio, and the p value of the f distribution. P values are significant $p < 0.05$.

Trait	**DF Model 1**	**DF Model 2**	**f**	**p (>f)**
Height	142	153	0.4418	0.9346
Tiller	142	153	1.6722	0.08545
$(AGBM)^2$	142	153	0.9233	0.5199
SR	142	153	0.8128	0.6273
LOG(BGBM+1)	141	152	0.7575	0.6815
R:S	138	149	0.9651	0.4811
β	129	140	1.2446	0.2644
$(SRL)^2$	795	818	1.1739	0.2602
$(RTD)^2$	795	818	0.5793	0.9431
RDIA	558	605	0.7232	0.9161

Table S3 Shapiro-Wilk normality test and Levene's test of homogeneity of variances of; aboveground traits, height, number of tillers AGBM; architectural traits, SR, β, R:S and BGBM; and morphological traits, SRL, RTD and RDIA, of the teff genotypes. W tests values, p values, and transformed values are reported for all traits. P values are significant on a level ($p < 0.05$).

		Shapiro-Wilk			Levene's test	
Trait:	**W-value**	**W-value, log/sqrt**	**p-value**	**p-value, log/sqrt**	**p-value**	**p-value, log/sqrt**
Height	0.995	-	0.837	-	32.7E-3	-
Tiller	0.984	-	0.050	-	1.5E-2	-
AGBM	0.979	0.995	0.014	0.821	0.323	0.673
SR	0.990	-	0.257	-	0.617	-
BGBM	0.979	0.994	0.013	0.682	0.304	0.611
R:S	0.989	-	0.243	-	0.761	-
β	0.984	-	0.075	-	0.245	-
SRL	0.985	0.996	45.6E-7	0.099	73.2E-6	0.088
RTD	0.982	0.996	52.8E-7	0.063	0.135	0.154
DIAM	0.985	0.987	40.1E-6	98.7E-6	0.098	0.083

Table S4 Detailed data on mean values of morphological root traits SRL, RTD and RDIA, of six teff genotypes under two nitrogen regimes N+ and N-. All root traits are represented at root depth increments of 20 cm. Values are reported as mean ± SE.

Genotype	Depth	SRL ($m\ g^{-1}$)		RTD ($g\ cm^{-3}$)		RDIA (mm)	
		N+	N-	N+	N-	N+	N-
Addisie	0-20	328.95 ± 16.01	311.82 ± 22.19	0.095 ± 0.006	0.090 ± 0.004	0.2102 ± 0.007	0.2109 ± 0.006
	20-40	435.70 ± 20.52	368.59 ± 10.68	0.078 ± 0.003	0.072 ± 0.004	0.1992 ± 0.006	0.2169 ± 0.007
	40-60	397.27 ± 18.98	426.74 ± 24.80	0.087 ± 0.006	0.082 ± 0.005	0.2027 ± 0.008	0.1981 ± 0.007
	60-80	403.67 ± 15.73	357.04 ± 9.71	0.090 ± 0.004	0.090 ± 0.006	0.1866 ± 0.003	0.2078 ± 0.005
	80-100	327.98 ± 13.28	344.52 ± 22.65	0.079 ± 0.003	0.079 ± 0.004	0.2282 ± 0.008	0.2271 ± 0.008
Alba	0-20	298.86 ± 13.24	308.46 ± 20.04	0.096 ± 0.005	0.083 ± 0.005	0.2134 ± 0.006	0.2292 ± 0.008
	20-40	390.53 ± 24.18	449.05 ± 22.90	0.075 ± 0.007	0.065 ± 0.003	0.2110 ± 0.006	0.2060 ± 0.009
	40-60	487.80 ± 25.81	440.69 ± 26.47	0.076 ± 0.006	0.076 ± 0.006	0.1894 ± 0.005	0.2057 ± 0.008
	60-80	399.83 ± 16.74	406.40 ± 13.49	0.082 ± 0.006	0.078 ± 0.003	0.1981 ± 0.009	0.1967 ± 0.007
	80-100	407.32 ± 18.57	442.44 ± 19.37	0.070 ± 0.002	0.067 ± 0.005	0.2168 ± 0.007	0.2157 ± 0.006
Balami	0-20	260.74 ± 18.32	340.83 ± 16.67	0.092 ± 0.006	0.093 ± 0.006	0.2404 ± 0.004	0.2106 ± 0.010
	20-40	393.51 ± 39.48	339.17 ± 28.93	0.074 ± 0.003	0.076 ± 0.010	0.2204 ± 0.010	0.2265 ± 0.009
	40-60	405.47 ± 21.56	431.41 ± 21.38	0.070 ± 0.003	0.064 ± 0.004	0.2118 ± 0.009	0.2268 ± 0.009
	60-80	384.41 ± 11.40	404.29 ± 20.88	0.075 ± 0.005	0.069 ± 0.005	0.2144 ± 0.009	0.2170 ± 0.008
	80-100	295.98 ± 20.10	396.91 ± 26.96	0.084 ± 0.005	0.068 ± 0.004	0.2353 ± 0.007	0.2289 ± 0.008
Beten	0-20	302.41 ± 19.85	296.35 ± 11.20	0.092 ± 0.006	0.094 ± 0.008	0.2259 ± 0.008	0.2168 ± 0.007
	20-40	354.48 ± 22.52	369.49 ± 24.22	0.075 ± 0.005	0.075 ± 0.005	0.2212 ± 0.009	0.2174 ± 0.008
	40-60	362.24 ± 15.54	370.36 ± 10.43	0.080 ± 0.005	0.079 ± 0.004	0.2116 ± 0.010	0.2140 ± 0.006
	60-80	353.80 ± 11.10	338.98 ± 16.54	0.083 ± 0.003	0.082 ± 0.007	0.2107 ± 0.006	0.2246 ± 0.008
	80-100	325.63 ± 19.25	317.25 ± 25.42	0.073 ± 0.004	0.059 ± 0.003	0.2397 ± 0.008	0.2742 ± 0.008
T10	0-20	315.17 ± 18.59	323.16 ± 10.65	0.089 ± 0.006	0.087 ± 0.006	0.2168 ± 0.010	0.2109 ± 0.008
	20-40	454.02 ± 27.81	456.04 ± 30.35	0.067 ± 0.004	0.071 ± 0.003	0.2075 ± 0.010	0.2073 ± 0.008
	40-60	436.50 ± 22.78	429.78 ± 19.94	0.082 ± 0.007	0.076 ± 0.006	0.1915 ± 0.007	0.2063 ± 0.006
	60-80	401.75 ± 19.58	444.77 ± 27.48	0.076 ± 0.005	0.080 ± 0.007	0.2071 ± 0.004	0.1951 ± 0.009
	80-100	429.64 ± 27.88	357.29 ± 27.66	0.069 ± 0.003	0.079 ± 0.007	0.2136 ± 0.008	0.2273 ± 0.010
T11	0-20	333.23 ± 25.99	392.26 ± 33.62	0.085 ± 0.005	0.086 ± 0.005	0.2135 ± 0.008	0.2046 ± 0.008
	20-40	421.19 ± 35.66	479.82 ± 36.18	0.079 ± 0.006	0.075 ± 0.006	0.1976 ± 0.009	0.1991 ± 0.011
	40-60	426.05 ± 32.20	470.73 ± 19.24	0.079 ± 0.006	0.066 ± 0.005	0.1946 ± 0.007	0.2240 ± 0.011
	60-80	418.76 ± 22.88	444.89 ± 25.69	0.081 ± 0.005	0.077 ± 0.007	0.2053 ± 0.009	0.2034 ± 0.010
	80-100	401.42 ± 46.90	416.46 ± 38.61	0.076 ± 0.007	0.064 ± 0.004	0.2239 ± 0.008	0.2311 ± 0.008

Table S5 P values of correlation coefficients in the pairwise correlation matrix of all traits Height, number of tillers, aboveground biomass (AGBM), seminal root number (SR), belowground biomass (BGBM), value (β), root shoot ratio (R:S), specific root length (SRL) root tissue density (RTD), and root diameter (RDIA), of the teff genotypes. Correlations are evaluated as; Spearman's rank correlations are significant at ($p < 0.05$).

	Height	**Tiller**	**AGBM**	**SR**	**BGBM**	**β**	**R:S**	**SRL**	**RTD**	**RDIA**
RDIA										1
RTD									1	0.0485
SRL								1	0.6489	0.0410
R:S							1	0.9711	0.8255	0.8759
β						1	0.0472	0.5809	0.9532	0.7534
BGBM					1	0.5343	0.0693	0.3121	0.1465	0.7563
SR				1	0.0001	0.3531	0.0175	0.3726	0.3144	0.9406
AGBM			1	0.0000	0.0002	0.2042	0.0013	0.5396	0.3220	0.7886
Tiller		1	0.6374	0.7767	0.9729	0.1354	0.3210	0.8528	0.9226	0.9579
Height	1	0.0509	0.0037	0.0224	0.0448	0.0710	0.0015	0.6552	0.6176	0.8704